Nekton Densities in Shallow Estuarine Habitats of Texas and Louisiana and the Identification of Essential Fish Habitat

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Abstract.—The Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens) Act) of 1996 requires the identification of essential fish habitat (EFH) for fishery species under federal fishery management plans (FMPs). As defined in the Magnuson-Stevens Act, EFH includes waters and substrate necessary for spawning, breeding, feeding, or growth to maturity. Without EFH, fishery species will be unable to maintain the productivity needed to support a sustainable fishery or contribute ecologically to aquatic ecosystems. The highly productive estuaries in the northern Gulf of Mexico contain many habitat types that are potentially essential for species under FMPs such as brown shrimp *Penaeus aztecus*, white shrimp *P. setiferus*, pink shrimp *P. duorarum*, gulf stone crab Menippe adina, red drum Sciaenops ocellatus, gray snapper Lutjanus griseus, and bluefish Pomatomus saltatrix; these species spend their juvenile life stages in estuarine nurseries. Estuarine habitats also may be important for prey required as forage by managed species and for other fishery species not under FMPs. My objective in this paper was to summarize information on densities of juvenile fishery species and other animals (all generally <100 mm total length) in shallow-water estuarine areas of Texas and Louisiana. I attempted to identify where these species live (delineate their habitat) and to analyze density patterns within habitats that would be useful in distinguishing EFH. My analysis was restricted to data collected with enclosure sampling techniques because these techniques have been shown to provide comparable density estimates among highly diverse shallow-water areas. Habitat types evaluated included Spartina alterniflora marsh edge (SAME), mixed-vegetation marsh edge, inner marsh (>5 m from open water), submerged aquatic vegetation (SAV), oyster reefs, and shallow nonvegetated bottom (SNB). Data also were categorized by season, salinity regime, estuarine system, and year of collection. Mean densities among habitat types frequently varied in relation to salinity regime, but overall, SAME was used most by brown shrimp, white shrimp, blue crab Callinectes sapidus, spotted seatrout Cynoscion nebulosus, and southern flounder Paralichthys lethostigma. Highest densities of pink shrimp, red drum, and sand seatrout Cynoscion arenarius were found in SAV. Stone crabs had highest mean densities on oyster reefs and gulf menhaden Brevoortia patronus on SNB. Each of the six habitat types examined ranked first or second in use by at least one of these fishery species. Thus, all of these habitat types are likely essential for some fishery species. The analysis highlighted many of the challenges confronted in determining habitat-use patterns and emphasized the need for additional systematic sampling to examine geographic variability in habitat use and to examine distribution patterns within habitats. However, in addition to analyses of intrahabitat densities, the identification of EFH requires information on functional relationships between fishery species and habitat characteristics.

Despite evidence of important ecological linkages between environmental conditions and fishery production, the management of commercial fishery resources in the United States has historically concentrated on assessing stock size and controlling fishing mortality. However, under the Magnuson-Stevens Fishery Conservation and Management Act of 1996 (Magnuson-Stevens Act), the conservation and management of fishery habitat became an important component of comprehensive fishery management programs. The Magnuson-Stevens Act directs fishery management councils and the National Marine Fisheries Service to identify essential fish habitat

(EFH) for all managed fishery species and to identify adverse impacts, actions to ensure conservation and enhancement, and approaches to the restoration of EFH. Essential fish habitat is defined in the Magnuson-Stevens Act as waters and substrate necessary for spawning, breeding, feeding, or growth to maturity. Without EFH, fishery species will be unable to maintain the productivity needed to support a sustainable fishery or contribute ecologically to aquatic ecosystems (62 FR 66531) (NMFS 1997).

An organism's habitat is the place where it lives (Odum 1971; Whitaker and Levin 1975; Baltz 1990; Peters and Cross 1992; Ricklefs 1993). From this

44

simple definition, two important concepts ensue: (1) that at any particular life stage, a species has one habitat and (2) that an organism defines its habitat by its spatial distribution. Ecologists attempt to describe the habitat of a species based on characteristics known to be ecologically meaningful; for fishery species these characteristics often include structure (e.g., vegetation type, rock outcroppings); substrate (sediment grain size, organic content); hydrodynamics (currents, tidal flooding patterns); and general hydrology (depth, temperature, salinity, turbidity). Accurately identifying the habitat for each life stage of a fishery species is a crucial first step in identifying EFH, because areas that are not habitats are not essential habitats. In addition, however, some parts of a species' habitat may not be essential for maintaining that species' productivity.

In the Gulf of Mexico, many abundant fishery species that live and spawn in coastal waters have young that migrate into estuarine nursery grounds where they grow into subadults. Habitats in estuaries are likely to contribute substantially to the productivity of these fishery species because estuarine ecosystems have some of the highest levels of primary production observed. The general link between environmental conditions in Gulf estuaries and fishery production has been recognized for some time (Gunter 1941, 1961; Hildebrand and Gunter 1953; St. Amant et al. 1962; Zein-Eldin 1963). Indeed, production of shrimp has been correlated on a large scale with the amount of coastal wetlands in the region (Turner 1977). For most species, however, specific habitats used within estuaries have not been adequately defined, and the portions of these habitats that are essential in maintaining fishery production have not been identified.

The juveniles of fishery species that use estuaries as nursery grounds are only temporary residents and transient members of estuarine communities (Deegan and Thompson 1985; Kneib 1997). These juveniles often appear to be ubiquitously distributed within estuaries, and the entire estuary might be their habitat. A habitat delineation of the entire estuary, however, does little to identify functional relationships or important interactions with habitat characteristics, and, therefore, such a delineation does little to assist us in identifying essential portions of a habitat. It is necessary to subdivide this habitat into smaller parcels (termed "intrahabitat" areas here) that have distinct features important to fishery species. We can identify these important intrahabitat areas by examining density patterns within the habi-

tat or by examining relationships between habitat characteristics and life history functions such as growth, survival, and reproduction. Some of the most commonly examined intrahabitat areas are associated with well-recognized ecological communities within estuaries such as sea grass beds, oyster reefs, salt marshes, mangroves, tidal mudflats, and subtidal bay bottom; these community habitats are termed biotopes (Whitaker et al. 1973). The estuarine habitat of a species can also be divided into different intrahabitat areas based on other characteristics. For example, both animals and plants have different tolerances to salinities found within estuaries, and the use of the above biotopes by a fishery species can change in relation to salinity regimes (Zimmerman et al. 1990a, 1990b). Within intertidal marsh, elevation and proximity to open water also appear to affect use patterns and habitat value for some fishery species (Rozas and Reed 1993; Minello et al. 1994; Peterson and Turner 1994; Minello and Webb 1997). On nonvegetated bottom, water depth affects habitat use (Ruiz et al. 1993), and differences in sediment texture have been related to differences in shrimp (Williams 1958; Rulifson 1981) and fish (Keefe and Able 1994; Moles and Norcross 1995) distributions.

My objective in this paper is to improve our ability to delineate habitats of juvenile fishery species and other small nekton (all generally <100 mm total length or carapace width) in shallow estuarine areas of Texas and Louisiana. The density database developed for this purpose was restricted to data collected with enclosure sampling techniques because these techniques provide comparable density estimates among highly diverse biotopes (Rozas and Minello 1997). Samples were classified into six habitat types including submerged aquatic vegetation, Spartina alterniflora marsh edge, mixedvegetation marsh edge, inner marsh, shallow nonvegetated bottom, and oyster reefs. Mean nekton densities were calculated for these habitat types; for fishery species, densities in different salinity regimes were also examined. On the basis of utilization patterns, I speculate on the relative importance of these intrahabitat areas and their possible designation as EFH.

Methods

Data were collected from 22 studies where enclosure samplers were used in estuarine habitats of Texas and Louisiana including published work by Zimmerman et al. (1984, 1989, 1990a, 1990b); Zimmerman and Minello (1984); Thomas et al. (1990);

Czapła (1991); Minello et al. (1991); Minello and Zimmerman (1992); Rozas and Reed (1993); Peterson and Turner (1994); Minello and Webb (1997); Rozas and Minello (in press); and unpublished study results from the Galveston Laboratory of the National Marine Fisheries Service. Over 5,000 samples were classified into the following habitat types:

- Spartina alterniflora marsh edge (SAME)—defined as intertidal S. alterniflora marsh within 5 m of open water;
- Mixed-vegetation marsh edge (MVME)—defined as above but with various other species of vegetation including Spartina patens, Juncus roemerianus, Scirpus spp., Typha, and Distichlis spicata;
- Inner marsh—defined as marsh more than 5 m from open water and including *S. alterniflora* or *Distichlis spicata*;
- Submerged aquatic vegetation (SAV)—including Thalassia testudinum, Halodule wrightii, Syringodium filiforme, Halophila engelmanni, or Ruppia maritima;
- Oyster reef—consisting of low intertidal areas along Confederate Reef in the Galveston Bay system of Texas;
- Shallow nonvegetated bottom (SNB)—generally restricted to water <1 m deep including creeks, ponds, shoreline, and open bay areas. Shallow nonvegetated bottom was mostly subtidal except for the shallowest areas on extreme low tides.

For each study, density data for fishes and decapod crustaceans were incorporated into the database as mean values (number per m²) after characterizing the samples by habitat type, year, season, salinity regime, and estuarine system. Size or biomass data were not included in the database. However, I have reported mean sizes for some common fishery species based on samples in the database collected in Galveston Bay. These data and published size data by Zimmerman and Minello (1984), Thomas et al. (1990), Czapla (1991), and Rozas and Minello (in press) indicate that the vast majority of organisms represented in the database were less than 100 mm in total length (TL) or carapace width (CW). Therefore, although the database included most life stages of small resident species, only the juveniles of transient fishery species were represented.

Spring samples were those samples collected in March, April, and May; summer samples were collected in June, July, and August; fall samples were collected in September, October, and November; and winter samples were collected in December, January, and February. Estuaries were divided into salinity zones based on long-term patterns in each system (Orlando et al. 1991, 1993), and these zones were defined as oligohaline (annual mean salinity between 0.5 and 5.0 parts per thousand [ppt]), mesohaline (5–18 ppt), polyhaline (18–30 ppt), and euhaline (30–40 ppt). The different estuaries sampled along the coast were consolidated into the following systems: Lower Laguna Madre (LLM); Upper Laguna Madre (ULM); Corpus Christi Bay (CCB); Redfish, Aransas, Copano, and Mesquite Bays (AB); San Antonio Bay and Espiritu Santo Bay (SAB); Matagorda Bay (MB); Galveston Bay system (GB); Terrebonne and Timbalier Bays (TB); and Barataria Bay (BB). (See Figure 1 for the locations of these systems.)

In addition to the mean density, the standard error was included in the database for the number of samples collected in a study for each habitat type, year, season, salinity regime, and estuary combination. The number of samples (N) collected and used to calculate the mean was also recorded. In addition, a location variable was included for each mean to indicate the number of different locations sampled. The difference between replicate samples at one location and sampling two locations is one of scale. If samples were separated by a distance of approximately 2 km or more, they were considered to be from different locations. The number of locations sampled for each habitat type was 184 for SAME, 132 for SAV, 183 for SNB, 61 for MVME, 22 for inner marsh, and 2 for oyster reef. The area used for the density determination (area enclosed or sampled each time the gear was deployed) and the type of gear used to collect the samples was listed in the database. The tide level at the time of sampling also was recorded because animal densities in shallowwater areas of the estuary are affected by tidal flood stage (Rozas and Minello 1997).

No formal statistical tests were used to compare means among intrahabitat areas. The mean nekton density for any area was calculated as the mean of the means included in the database for that intrahabitat area. Use of these weighted means reduced the influence of any one study on density patterns; this approach is similar to that used in a meta-analysis. The variability, or standard error (SE), presented in this chapter also was calculated using the means as observations. This variability within habitat types was often quite high because it incorporated differences related to years, seasons, salinity regimes, and estuaries. I considered

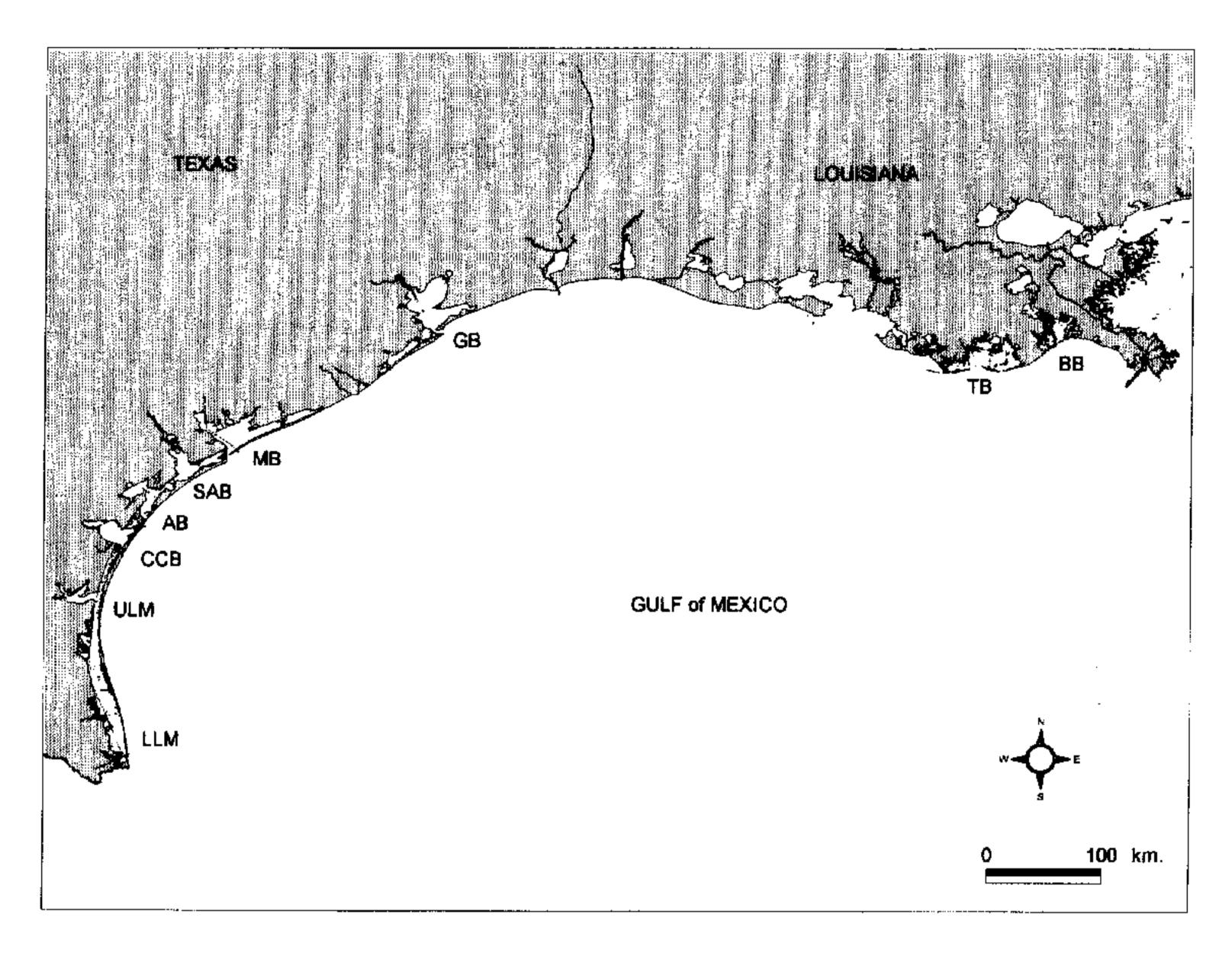


FIGURE 1.—Estuaries of Texas and Louisiana where data were collected on densities of fishery species and other nekton. Estuaries were consolidated into the following systems: Lower Laguna Madre (LLM); Upper Laguna Madre (ULM); Corpus Christi Bay (CCB); Redfish, Aransas, Copano, and Mesquite Bays (AB); San Antonio Bay and Espiritu Santo Bay (SAB); Matagorda Bay (MB); Galveston Bay system (GB); Terrebonne and Timbalier Bays (TB); and Barataria Bay (BB).

the use of a factorial analysis of variance (ANOVA) to partition this residual error, but the unbalanced nature of the data and the common occurrence of missing cells (treatment combinations with no data) made comparisons of main-effect means difficult (Milliken and Johnson 1984; Day and Quinn 1989). In addition, the data did not meet the ANOVA assumption of homogeneity in variances even following logarithmic transformation. If desired, limited statistical comparisons of means could be made using simple *t*-tests. The results of such tests should be quite conservative for the above reasons and because each mean generally represents a substantial number of samples.

Results

General Description of the Database

The database contained a total of 350 mean density values for every taxon found in each of the 5,149 samples represented. The most frequently sampled habitat types were *Spartina alterniflora* marsh edge, shallow nonvegetated bottom, and submerged

aquatic vegetation (Table 1). Shallow nonvegetated bottom included creeks and ponds (samples collected) within a marsh complex and surrounded by vegetation), shore (samples collected along semiprotected or exposed bay shorelines), and open water (a small number of samples collected at least 100 m from any shoreline). These nonvegetated samples were also characterized in the database on the basis of general substrate texture (mud versus sand). Submerged aquatic vegetation included four species of sea grasses and widgeongrass Ruppia maritima; the most frequently sampled type of SAV was shoalgrass Halodule wrightii. About 3% of the SAV samples were taken on areas of dredged material. The age of these beds is unknown, but they were at least five years old at the time of sampling. Mixed-vegetation marsh edge was represented by 258 samples and more than six species of marsh vegetation. Inner marsh (defined as areas more than 5 m away from open water) was vegetated by either S. alterniflora or Distichlis spicata. Oyster reefs were not well represented in the database, and data were recorded from only 16 samples (one study).

TABLE 1.—The number of mean density values and the total number of samples (in parentheses) represented in the database for each habitat type (in bold type) and each season.

	<u> </u>	Se	eason		
Habitat type	Spring	Summer	Fall	Winter	Total
Submerged aquatic vegetation (SAV)	33 (469)	8 (192)	32 (367)	2 (60)	75 (1,088)
Halodule wrightii	15 (320)	7 (184)	12 (232)	2 (60)	36 (796)
Halodule wrightii on old spoil	2 (6)	0 (0)	1 (3)	0 (0)	3 (9)
Halodule and Ruppia	5 (55)	0 (0)	9 (75)	0 (0)	14 (130)
Halophila engelmanni on old spoil	1 (4)	0 (0)	0 (0)	0 (0)	1 (4)
Ruppia maritima	2 (8)	1 (8)	3 (12)	0 (0)	6 (28)
Syringodium filiforme	4 (38)	0 (0)	3 (20)	0 (0)	7 (58)
Syringodium filiforme on old spoil	1 (8)	0 (0)	1 (3)	0 (0)	2 (11)
Thalassia testudinum	2 (24)	0 (0)	2 (16)	0 (0)	4 (40)
Thalassia testudinum on old spoil	1 (6)	0 (0)	1 (6)	0 (0)	2 (12)
Spartina alterniflora marsh edge (SAME)	39 (616)	22 (397)	36 (571)	12 (214)	109 (1,798)
Aixed vegetation marsh edge (MVME)	14 (87)	8 (51)	18 (120)	0 (0)	40 (258)
Distichlis spicata	3 (8)	3 (21)	1 (15)	0 (0)	7 (44)
Juncus roemerianus	5 (44)	2 (9)	5 (46)	0 (0)	12 (99)
Phragmites australis	1(1)	0 (0)	0 (0)	0 (0)	1(1)
S. alterniflora and Typha	1 (4)	0 (0)	1 (4)	0 (0)	2 (8)
S. alterniflora, Typha and Scirpus	0 (0)	0 (0)	3 (12)	0 (0)	3 (12)
Scirpus maritimus	2 (14)	2 (13)	2 (11)	0 (0)	6 (38)
Scirpus spp.	1 (8)	1 (8)	1 (8)	0 (0)	3 (24)
Scirpus and Hyacinth	0 (0)	0 (0)	1 (4)	0 (0)	1 (4)
Scirpus and S. alterniflora	0 (0)	0 (0)	1 (4)	0 (0)	1 (4)
Spartina patens	1 (8)	0 (0)	3 (16)	0 (0)	4 (24)
nner marsh	5 (55)	4 (81)	4 (65)	1 (18)	14 (219)
Distichlis spicata	1 (2)	1 (5)	0 (0)	0 (0)	2 (7)
S. alterniflora	4 (53)	3 (76)	4 (65)	1 (18)	12 (212)
Dyster reef	0 (0)	1 (8)	0 (0)	1 (8)	2 (16)
Shallow nonvegetated bottom	36 (589)	24 (416)	41 (589)	9 (176)	110 (1,770)
Creeks and ponds, mud	3 (52)	2 (24)	3 (52)	0 (0)	8 (128)
Open water, mud	0 (0)	1 (8)	0 (0)	1 (8)	2 (16)
Open water, sand	1 (24)	2 (24)	1 (16)	1 (24)	5 (88)
Shore, creeks, ponds, sandy mud	9 (286)	9 (237)	9 (221)	7 (144)	34 (888)
Shore, open water, muddy sand	1 (35)	0 (0)	1 (35)	0 (0)	2 (70)
Shore, mud	7 (36)	2 (18)	9 (52)	0 (0)	18 (106)
Shore, sandy mud	9 (114)	6 (78)	12 (170)	0 (0)	27 (362)
Shore, sand	5 (30)	2 (27)	6 (43)	0 (0)	13 (100)
Shore, muddy sand	1 (12)	0 (0)	0 (0)	0 (0)	1 (12)
Total .	127 (1,816)	67 (1,145)	131 (1,712)	25 (476)	350 (5,149

Most of the samples used in this analysis were collected in the spring and fall (68% of total), but the summer season was also well represented (Table 1). Few samples (9%) were collected during the winter, mainly because few organisms occur in these

shallow-water estuarine areas during the cold months of the year. The distribution of sampling effort among seasons was similar for most habitat types. Samples in oyster reefs, however, were only collected in the summer and winter.

TABLE 2.—The number of mean density values and the total number of samples (in parentheses) represented in the database for each salinity regime and habitat type.

Summary habitat	Euhaline	Polyhaline	Mesohaline	Oligohaline	Total
Submerged aquatic vegetation (SAV)	35 (434)	29 (606)	5 (20)	6 (28)	75 (1,088)
Spartina alterniflora marsh edge (SAME)	1 (4)	77 (1,484)	25 (291)	6 (19)	109 (1,798)
Mixed vegetation marsh edge (MVME)	0 (0)	5 (32)	17 (145)	18 (81)	40 (258)
Inner marsh	0 (0)	2 (20)	12 (199)	0 (0)	14 (219)
Oyster reef	0 (0)	2 (16)	0 (0)	0 (0)	2 (16)
Shallow nonvegetated bottom (SNB)	0 (0)	73 (1,402)	23 (268)	14 (100)	110 (1,770)
Total	36 (438)	188 (3,560)	82 (923)	44 (228)	350 (5,149)

The sampling effort represented in the database was concentrated in the polyhaline zone of estuaries, and 69% of the samples (54% of means) were collected in this salinity regime (Table 2). Mesohaline areas of estuaries were represented by 18% of the samples, while the remaining samples were split about evenly between euhaline and oligohaline areas. This distribution of sampling effort among salinity regimes was similar for most habitat types, with the important exception of SAV. Almost all SAV samples (96%) were collected in euhaline or polyhaline salinity regimes, and almost all samples in the euhaline salinity regime (prima-

rily in the Laguna Madre of South Texas) were in SAV. Submerged aquatic vegetation is common in many oligohaline and tidal freshwater areas of these estuaries, but few samples (all widgeongrass) were available from these areas.

Seven estuarine systems in Texas were represented in the database (94% of samples), as well as two systems (6% of samples) from Louisiana (Figure 1; Table 3). Within Texas, most of the samples were collected in the Galveston Bay system (74%). The south Texas coast is relatively arid, and most of the estuaries in this region have large euhaline zones; samples from the Laguna Madre and Corpus Christi

TABLE 3.—The number of mean density values and the total number of samples (in parentheses) represented in the database for each estuary, habitat type, and salinity regime. Abbreviations for habitat types are shown in Tables 1 and 2.

			Ha	bitat type				
Estuary	Salinity regime	SAV	SAME	MVME	Inner marsh	Oyster	SNB	Total
Lower Laguna Madre (LLM)	Euhaline	29 (264)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	29 (264)
Upper Laguna Madre (ULM)	Euhaline	6 (170)	0 (0)	0 (0)	0(0)	0 (0)	0 (0)	6 (170)
Corpus Christi Bay (CCB)	Euhaline	0 (0)	1 (4)	0(0)	0 (0)	0 (0)	0 (0)	1 (4)
Aransas Bay Complex (AB)	Polyhaline	2 (70)	2 (60)	0 (0)	0 (0)	0 (0)	2 (70)	6 (200)
San Antonio Bay (SAB)	Polyhaline	7 (40)	6 (36)	1 (4)	0(0)	0 (0)	7 (40)	21 (120)
	Mesohaline	5 (20)	6 (24)	1 (4)	0(0)	0 (0)	7 (28)	19 (76)
	Oligohaline	3 (12)	3 (12)	5 (20)	0 (0)	0 (0)	7 (32)	18 (76)
Matagorda Bay,	Polyhaline	0 (0)	6 (50)	2(8)	0(0)	0 (0)	5 (58)	13 (116)
mainly Lavaca (MB)	Mesohaline	0 (0)	3 (9)	8 (63)	0(0)	0 (0)	6 (76)	17 (148)
	Oligohaline	0 (0)	2 (3)	10 (37)	0(0)	0 (0)	3 (40)	15 (80)
Galveston Bay (GB)	Polyhaline	20 (496)	62 (1,328)	2 (20)	2 (20)	2 (16)	58 (1,224)	146 (3,104)
	Mesohaline	0 (0)	9 (192)	5 (40)	3 (24)	0 (0)	10 (164)	27 (420)
	Oligohaline	3 (16)	1 (4)	3 (24)	0(0)	0 (0)	4 (28)	11 (72)
Terrebonne and								
Timbalier Bays (TB)	Mesohaline	0(0)	7 (66)	3 (38)	9 (175)	0 (0)	0 (0)	19 (279)
Barataria Bay (BB)	Polyhaline	0 (0)	1 (10)	0 (0)	0 (0)	0 (0)	1 (10)	2 (20)
Total		75 (1,088)	109 (1,798)	40 (258)	14 (219)	2 (16)	110 (1,770)	350 (5,149)

Bay were only collected in euhaline salinity regimes and were almost exclusively from SAV. The widest salinity ranges were represented in estuaries located on the central to northern coast of Texas. Inner marsh and oyster reef samples were collected only in one or two estuarine systems.

Samples in the database were collected between the years 1982 and 1997. All years except 1992 were represented, and the distribution of samples among years was relatively even. The majority of samples (84%) in the database were collected with either a 1-m² or 2.6-m² drop sampler (Zimmerman et al. 1984). Other gear used included flumes (Peterson and Turner 1994), lift nets (Rozas and Reed 1993), and throw traps. Most samples (84%) were collected when tide levels were high and intertidal vegetation was flooded.

Especially for uncommon species, the number of means recorded in these summary data are less than the possible number of means based on sampling effort. This situation reflects a problem distinguishing between zeros and missing data. I could not always determine whether the lack of a species in a list of animals meant that it was not present in the sample or that it was not identified. In this situation, I assumed that the species was not present (zero density) if that species was identified from other samples in the study. I did not include a zero for the density of a species if it was not identified in a particular study, even though this often would have been appropriate. Therefore, the count of means for the less-common species is a minimum value. Mean densities for these species would be lower than those reported here if I had included all zeros for samples from studies where the species was not identified.

General Density Patterns in Different Habitat Types

The database included over 20,000 records of mean densities for various species collected in shallow waters of these estuaries, and these means provided general information on habitats of species and on utilization patterns within habitats (Tables 4 and 5). Decapod crustaceans were the most abundant organisms (Table 4), and 54 taxa were identified including 48 species and 6 species complexes (e.g., Callinectes spp.). Grass shrimps in the genus Palaemonetes (estuarine residents) were by far the most abundant crustaceans; this genus was collected mainly within vegetated areas. The blue crab Callinectes sapidus and its congeners along with

brown shrimp *Penaeus aztecus* ¹ and white shrimp P. setiferus (also known as Penaeus setiferus) were also relatively abundant. Although rankings varied, these abundant crustaceans were generally dominant in vegetated areas and on shallow nonvegetated bottom (Table 6). The dominant crustaceans on oyster reefs were small resident crabs including the green porcelain crab *Petrolisthes armatus* and the xanthid crabs Panopeus herbstii and Eurypanopeus depressus. Crustacean species in the database under federal fishery management plans (FMPs) included brown shrimp, white shrimp, pink shrimp P. duorarum (also known as Penaeus duorarum), and gulf stone crab Menippe adina. There is also an active fishery for blue crab in Texas and Louisiana. Many of the other crustaceans in the database are prey for fishery species.

Compared with crustaceans, fishes were less abundant but more diverse; 86 species and 2 species complexes were identified in samples (Table 5). On the basis of mean density from all samples, gulf menhaden Brevoortia patronus was the most abundant fish in these estuaries. This species was concentrated mainly in oligohaline salinity regimes, and mean densities were highest on shallow nonvegetated bottom and in marsh edge (Table 5). The naked goby Gobiosoma bosc was also abundant, and this small resident fish was ubiquitous, being a dominant species in all habitat types except inner marsh (Table 6). Inner marsh was dominated by gulf killifish Fundulus grandis, diamond killifish Adinia xenica, and the sheepshead minnow Cyprinodon variegatus (all estuarine residents). The pinfish Lagodon rhomboides was a dominant species in Spartina alterniflora marsh edge and in SAV, and bay anchovy Anchoa mitchilli was dominant on oyster reefs and shallow nonvegetated bottom. Only three fish species in the database are under federal FMPs; red drum Sciaenops ocellatus, gray snapper Lutjanus griseus, and bluefish *Pomatomus saltatrix*. However, the database included information on habitat-use patterns for other fishery species of both commercial and recreational importance in the region including gulf menhaden, southern flounder Paralichthys lethostigma, spotted seatrout Cynoscion nebulosus, and sand seatrout Cynoscion arenarius.

¹ Perez Farfante and Kensley (1997) have revised the scientific names of brown shrimp, pink shrimp, and white shrimp to *Farfantepenaeus aztecus*, *F. duorarum*, and *Litopenaeus setiferus*, respectively.

TABLE 4.—Mean densities of decapod crustaceans in different habitat types including submerged aquatic vegetation (SAV), Spartina alterniflora marsh edge (SAME), mixed vegetation marsh edge (MVME), inner marsh, oyster reef, and shallow nonvegetated bottom (SNB). Each mean density (animals per m²) was calculated as the mean of means in

Common name Mean SE Ct Mean SE Ct Mean SE Ct Mean SE Ct	Taxon		SAV			SAME		·	MVME	
Aceies americanus 1.599 0.483 71 0.322 0.000 3 0.004 0.003 32	(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Aphens heterochaetis 1.599 0.483 71 0.322 0.069 86 0.004 0.003 32 0.069 0.007	Crustaceans	50.216	8.724	75	83.540	6.500	109	36.037	5.627	40
Mapide device symmetricies 0.022 0.014 14 0.008 0.005 17 0.000 0.000 2 0.006 2 0.006 1 0.008 0.005 17 0.000 0.000 2 0.006 0.000 0.000 2 0.006 0.000 0.00	Acetes americanus			0	0.000	0.000	3			0
Ambidexter symmetricus	Alpheus heterochaelis	1.599	0.483	71	0.322	0.069	86	0.004	0.003	32
Ambidexter symmetricus	(bigclaw snapping shrimp)									
Callianassa jamaicensis 0.057 0.000 1 0.008 0.005 17 0.000 0.000 0.000 2 Callianassa spe. 0 0.000 0.000 0.000 1 0.000		0.022	0.014	14			0			0
Cestuarine ghost shrimp Calliansas aspp.	•	0.057	0.000	1	0.008	0.005	17	0.000	0.000	2
Callianassa spp. 0 0.000 0.000 1 0.000 0.000 0 0.000 0 0.000 0	_									
Callichirus major 0 0.000 0.000 6 0.000 0.000 7 Callinertes marants 0.013 0.013 15 0.000 0.00 15 0.000 0.00 7 Callinertes sapidlus 5.047 1.155 67 6.239 0.746 100 2.698 0.891 40 Callinertes sapidlus 0.675 0.145 58 0.096 0.065 21 0.022 0.014 9 Callinertes similis 0.675 0.145 58 0.096 0.065 21 0.022 0.012 9 Callinertes similis 0.675 0.145 8 3.980 1.969 8 0.022 0.010 3 Callinertes similis 0.112 0.030 71 0.0204 0.059 62 0.020 0.010 0.01 0.020 0.020 0.020 0.020 0.020 0.020 0.020 0.020 0.020 0.020 0.020 0.020 0.020 0.020	•			0	0.000	0.000	1	0.000	0.000	1
Callinectes ornanus (shellings) Callinectes sopidus (shellings) Callinectes similis (shellings) Callinectes similis (shellings) Callinectes spp. (shellings) Callinectes similis (shellings) Callinectes spp. (shellings) Callinectes similis (shellings	Callichirus major			0	0.000	0.000	6	0.000	0.000	2
Callinectes ornanus (shellings) Callinectes sopidus (shellings) Callinectes similis (shellings) Callinectes similis (shellings) Callinectes spp. (shellings) Callinectes similis (shellings) Callinectes spp. (shellings) Callinectes similis (shellings	(Carolinian ghost shrimp)									
Callinecter sapidus	_	0.013	0.013	15	0.000	0.000	15	0.000	0.000	7
Callinecter sapidus	(shelligs)									
Callinectes similis 0.675 0.145 58 0.096 0.065 21 0.022 0.014 9		5.047	1.155	67	6.239	0.746	100	2.698	0.891	40
Callinectes similis 0.675 0.145 58 0.096 0.065 21 0.022 0.014 9	•									
Callinectes spp. 13,746 2.614 8 3.980 1.969 8		0.675	0.145	58	0.096	0.065	21	0.022	0.014	9
Callinectes spp. 13,746 2.614 8 3.980 1.969 8	(lesser blue crab)									
Clibanarius vintatus 0.112 0.030 71 0.772 0.184 92 0.020 0.010 34	•	13.746	2.614	8	3.980	1.969	8			0
Disparanopeus texana 3.600 0.876 65 0.204 0.059 62 0.397 0.284 30 (gulf grassflat crab)	* *	0.112	0.030	71	0.772	0.184	92	0.020	0.010	34
Disparanopeus texana 3.600 0.876 65 0.204 0.059 62 0.397 0.284 30 (gulf grassflat crab)										
Companies of the property of	_ ` _ `	3.600	0.876	65	0.204	0.059	62	0.397	0.284	30
Eurypanopeus abbrevianus 0.000 0.000 7 0.032 0.020 6 0.000 0.000 31										
Clobate mud crab		0.000	0.000	7	0.032	0.020	6	0.000	0.000	3
Eurypanopeus depressus 0.009 0.009 22 0.042 0.017 56 0.000 0.000 31 (flatback mud crab)	-									
(flatback mud crab) Farfantepenaeus aztecus 7.341 1.026 54 7.479 0.699 104 2.598 0.574 40 (brown shrimp) Farfantepenaeus duorarum 1.563 0.702 30 1.050 0.238 73 0.498 0.296 31 (pink shrimp) Hippolyte zostericola 6.466 1.402 68 0.724 0.597 45 0.004 0.004 30 (zostera shrimp) Latreutes fucorum 0.013 0.013 15 0.002 0.000 1 0.000 0.000 23 (sangassum shrimp) Latreutes parvulus 0.013 0.013 15 0.002 0.002 19 0.000 0.000 23 (sangassum shrimp) Leander tenuicornis 0.000 0.000 8 0.001 0.001 12 0.000 23 (brown grass shrimp) Libinia dubia 0.049 0.017 44 0.010 0.004 37 0.000 0.000 23 (longnose spider crab) Littopenaeus setiferus 0.462 0.109 74 5.528 1.019 98 1.507 0.483 37 (white shrimp) Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp)	Eurypanopeus depressus	0.009	0.009	22	0.042	0.017	56	0.000	0.000	31
(brown shrimp) Farfantepenaeus duorarum 1.563 0.702 30 1.050 0.238 73 0.498 0.296 31 (pink shrimp) Hippolyte zostericola 6.466 1.402 68 0.724 0.597 45 0.004 0.004 30 (zostera shrimp) Latreutes fucorum 0 0.020 0.000 1 0	•									
Partantepenaeus duorarum 1.563 0.702 30 1.050 0.238 73 0.498 0.296 31 (pink shrimp) Hippotyte zostericola 6.466 1.402 68 0.724 0.597 45 0.004 0.004 30 (zostera shrimp) Latreutes fucorum 0.013 0.013 15 0.002 0.000 1 0.000 0.000 23 (slender sargassum shrimp) Latreutes parvulus 0.013 0.013 15 0.002 0.002 19 0.000 0.000 23 (sargassum shrimp) Leander tenuicornis 0.000 0.000 8 0.001 0.001 12 0.000 0.000 23 (brown grass shrimp) Libinia dubia 0.049 0.017 44 0.010 0.004 37 0.000 0.000 23 (longnose spider crab) Litopenaeus setiferus 0.462 0.109 74 0.5528 1.019 98 1.507 0.483 37 (white shrimp) Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 0.000 8 (estuarine longeye shrimp)	Farfantepenaeus aztecus	7.341	1.026	54	7.479	0.699	104	2.598	0.574	40
(pink shrimp) Hippolyte zostericola 6.466 1.402 68 0.724 0.597 45 0.004 0.004 30 Latreutes fucorum 0 0.020 0.000 1 0 0 (slender sargassum shrimp) Use ander tenuicornis 0.013 0.013 15 0.002 0.002 19 0.000 0.000 23 (sargassum shrimp) Use ander tenuicornis 0.000 0.000 8 0.001 0.001 12 0.000 0.000 23 (brown grass shrimp) Use ander tenuicornis 0.000 0.000 8 0.001 0.001 12 0.000 0.000 23 (brown grass shrimp) Use ander tenuicornis 0.000 0.001 0.001 0.001 12 0.000 0.000 23 Litanida dubia 0.049 0.017 44 0.010 0.004 37 0.000 0.000 23 Litopenaeus setiferus 0.462 0.109 74 5.528 1.019 98	(brown shrimp)									
Hippolyte zostericola (zostera shrimp) Latreutes fucorum (slender sargassum shrimp)	Farfantepenaeus duorarum	1.563	0.702	30	1.050	0.238	73	0.498	0.296	31
(zostera shrimp) Latreutes fucorum 0 0.020 0.000 1 0 <td>(pink shrimp)</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td>	(pink shrimp)									
Latreutes fucorum 0 0.020 0.000 1 0 (slender sargassum shrimp) 0.013 0.013 15 0.002 0.002 19 0.000 0.000 23 (sargassum shrimp) 0.000 8 0.001 0.001 12 0	Hippolyte zostericola	6.466	1.402	68	0.724	0.597	45	0.004	0.004	30
(slender sargassum shrimp) Latreutes parvulus 0.013 0.013 15 0.002 0.002 19 0.000 0.000 23 (sargassum shrimp) Leander tenuicornis 0.000 0.000 8 0.001 0.001 12 0 0 (brown grass shrimp) Libinia dubia 0.049 0.017 44 0.010 0.004 37 0.000 0.000 23 (longnose spider crab) Litopenaeus setiferus 0.462 0.109 74 5.528 1.019 98 1.507 0.483 37 (white shrimp) Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) Pachygrapsus g	(zostera shrimp)									
Latreutes parvulus 0.013 0.013 15 0.002 0.002 19 0.000 0.000 23 (sargassum shrimp) Leander tenuicornis 0.000 0.000 8 0.001 0.001 12 0	Latreutes fucorum			0	0.020	0.000	1			0
(sargassum shrimp) Leander tenuicornis 0.000 0.000 8 0.001 0.001 12 0 (brown grass shrimp) Libinia dubia 0.049 0.017 44 0.010 0.004 37 0.000 0.000 23 (longnose spider crab) Litopenaeus setiferus 0.462 0.109 74 5.528 1.019 98 1.507 0.483 37 (white shrimp) Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) Pachygrapsus gracilis 0 0.011 0.011 0.011 3 0 0	(slender sargassum shrimp)									
Leander tenuicornis 0.000 0.000 8 0.001 0.001 12 0 (brown grass shrimp) Libinia dubia 0.049 0.017 44 0.010 0.004 37 0.000 0.000 23 (longnose spider crab) Litopenaeus setiferus 0.462 0.109 74 5.528 1.019 98 1.507 0.483 37 (white shrimp) Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) Pachygrapsus gracilis 0 0.011 0.011 0.011 3 0 0	Latreutes parvulus	0.013	0.013	15	0.002	0.002	19	0.000	0.000	23
(brown grass shrimp) Libinia dubia 0.049 0.017 44 0.010 0.004 37 0.000 0.000 23 (longnose spider crab) 0.462 0.109 74 5.528 1.019 98 1.507 0.483 37 (white shrimp) 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) 0.004 0.011 0.011 3 0.000 0.001 3 0.000<	(sargassum shrimp)									
Libinia dubia 0.049 0.017 44 0.010 0.004 37 0.000 0.000 23 (longnose spider crab) Litopenaeus setiferus 0.462 0.109 74 5.528 1.019 98 1.507 0.483 37 (white shrimp) Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) Pachygrapsus gracilis 0 0.011 0.011 3 0 <t< td=""><td>Leander tenuicornis</td><td>0.000</td><td>0.000</td><td>8</td><td>0.001</td><td>0.001</td><td>12</td><td></td><td></td><td>0</td></t<>	Leander tenuicornis	0.000	0.000	8	0.001	0.001	12			0
(longnose spider crab) Litopenaeus setiferus 0.462 0.109 74 5.528 1.019 98 1.507 0.483 37 (white shrimp) Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) Pachygrapsus gracilis 0 0.011 0.011 3 0 0	(brown grass shrimp)									
Litopenaeus setiferus 0.462 0.109 74 5.528 1.019 98 1.507 0.483 37 (white shrimp) Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) Pachygrapsus gracilis 0 0.011 0.011 3 0	Libinia dubia	0.049	0.017	44	0.010	0.004	37	0.000	0.000	23
(white shrimp) Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris (estuarine longeye shrimp) 0.006 15 0.000 0.000 19 0.000 0.000 8 Pachygrapsus gracilis 0 0.011 0.011 3 0 0	(longnose spider crab)									
Macrobrachium ohione 0.026 0.026 15 0.024 0.014 21 0.288 0.288 7 (Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) Pachygrapsus gracilis 0 0.011 0.011 3 0	Litopenaeus setiferus	0.462	0.109	74	5.528	1.019	98	1.507	0.483	37
(Ohio shrimp) Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) Ogyrides alphaerostris (estuarine longeye shrimp) 0.006 15 0.000 0.000 19 0.000 0.000 8 Pachygrapsus gracilis 0 0.011 0.011 3 0 0	(white shrimp)									
Menippe adina 0.007 0.004 39 0.014 0.003 77 0.001 0.001 30 (gulf stone crab) 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) 0.001 0.011 0.011 3 0 0	Macrobrachium ohione	0.026	0.026	15	0.024	0.014	21	0.288	0.288	7
(gulf stone crab) Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) Pachygrapsus gracilis 0 0.011 0.011 3 0	(Ohio shrimp)									
Ogyrides alphaerostris 0.006 0.006 15 0.000 0.000 19 0.000 0.000 8 (estuarine longeye shrimp) 0 0.011 0.011 3 0	Menippe adina	0.007	0.004	39	0.014	0.003	77	0.001	0.001	30
(estuarine longeye shrimp) Pachygrapsus gracilis 0 0.011 0.011 3 0	(gulf stone crab)									
Pachygrapsus gracilis 0 0.011 0.011 3 0	Ogyrides alphaerostris	0.006	0.006	15	0.000	0.000	19	0.000	0.000	8
	(estuarine longeye shrimp)					•				
(dark shore crab)	Pachygrapsus gracilis			0	0.011	0.011	3			0
	(dark shore crab)									

TABLE 4. (cont.)—the database; also shown is the standard error (SE, calculated using means as observations) and the number of means (Ct = Count) used in the calculation. Data are included from all seasons, salinity regimes, estuaries, and years.

Taxon	Inn	er marsh	1	Oyste	er reef	·····		SNB			Total	
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Crustaceans	15.725	5.934	14	70.596	34.250	2	5.452	0.402	110	43.642	3.302	350
Acetes americanus			0			0	0.299	0.299	3	0.150	0.150	6
Alpheus heterochaelis	0.000	0.000	1	3.481	2.288	2	0.019	0.004	102	0.511	0.125	294
(bigelaw snapping shrimp)												
Ambidexter symmetricus			0			0	0.000	0.000	6	0.015	0.010	20
Callianassa jamaicensis (estuarine ghost shrimp)	0.000	0.000	2			0	0.077	0.047	18	0.040	0.022	40
Callianassa spp.	0.000	0.000	1			0	0.025	0.025	2	0.010	0.010	5
Callichirus major	0.000	0.000	1			0	0.013	0.008	7	0.006	0.004	16
(Carolinian ghost shrimp)												
Callinectes ornatus			0			0	0.000	0.000	21	0.003	0.003	58
(shelligs)												
Callinectes sapidus (blue crab)	0.526	0.123	14	0.231	0.077	2	0.902	0.099	109	3.543	0.364	332
Callinectes similis	0.000	0.000	2			0	0.105	0.053	34	0.362	0.075	124
(lesser blue crab)						•	31232			0.002	310.2	
Callinectes spp.			0			0	1.589	0.524	8	6.438	1.522	24
Clibanarius vittatus	0.033	0.033	3	1.212	0.904		0.099	0.037	108	0.299	0.059	310
(thinstripe hermit)	0.000	0.000	•	1.212	0.701	_	0.077	0.037	100	0.277	0.057	510
Dyspanopeus texana			0	0.000	0.000	2	0.031	0.013	74	1.125	0.267	233
(gulf grassflat crab)			J	0.000	0.000	_	0.051	0.013	, 4	1.125	0.207	233
Eurypanopeus abbreviatus			0			0	0.000	0.000	9	0.008	0.005	25
(lobate mud crab)			Ü			ŭ	0.000	0.000		0.000	0.005	20
Eurypanopeus depressus	0.000	0.000	1	13.577	9.731	2	0.012	0.005	68	0.170	0.131	180
(flatback mud crab)	0.000	0.000	•	13.377	7.751	_	0.012	0.005	00	0.170	0.131	100
Farfantepenaeus aztecus	0.452	0.240	14	0.000	0.000	2	1.879	0.190	109	4.611	0.336	323
(brown shrimp)												
Farfantepenaeus duorarum	0.000	0.000	1	0.019	0.019	2	0.131	0.030	86	0.674	0.133	223
(pink shrimp)												
Hippolyte zostericola			0			0	0.019	0.013	60	2.333	0.528	203
(zostera shrimp)												
Latreutes fucorum			0			0			0	0.020	0.000	1
(slender sargassum shrimp)												
Latreutes parvulus			0			0	0.000	0.000	26	0.003	0.002	83
(sargassum shrimp)												
Leander tenuicornis			0			0	0.000	0.000	12	0.000	0.000	32
(brown grass shrimp)												
Libinia dubia			0	0.000	0.000	2	0.000	0.000	42	0.017	0.005	148
(longnose spider crab)												
Litopenaeus setiferus	1.601	0.891	12	0.000	0.000	2	1.242	0.248	108	2.372	0.338	331
(white shrimp)								•		_		
Macrobrachium ohione			0			0	0.000	0.000	27	0.042	0.029	70
(Ohio shrimp)											_	
Menippe adina			0	1.885	0.731	2	0.002	0.001	88	0.023	0.012	236
(gulf stone crab)							-	-	-	- · -		- -
Ogyrides alphaerostris	0.000	0.000	1			0	0.006	0.006	26	0.004	0.003	69
(estuarine longeye shrimp)	-						-		_ ~		_ _	- -
Pachygrapsus gracilis			0			0	0.000	0.000	3	0.005	0.005	6
(dark shore crab)							_	_		_ 	_	

Table 4.—(continued).

Taxon		SAV			SAME			MVME	
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Pagurus annulipes	0.008	0.007	25			0			0
Pagurus criniticornis	0.296	0.104	37			0			0
Pagurus impressus	0.000	0.000	14			0			0
(dimpled hermit)									
Pagurus longicarpus	0.059	0.029	31	0.000	0.000	6			0
(longwrist hermit)									
Pagurus pollicaris	0.018	0.014	25	0.000	0.000	9			0
(flatclaw hermit)									
Palaemonetes intermedius	6.891	1.502	67	5.477	1.997	74	0.443	0.171	32
(brackish grass shrimp)									
Palaemonetes paludosus	0.846	0.688	15	2.705	1.991	15	0.000	0.000	7
(riverine grass shrimp)									
Palaemonetes pugio	11.637	4.005	67	58.753	5.070	96	25.655	4.903	40
(daggerblade grass shrimp)					 			.,,,	.0
Palaemonetes spp.	2.042	0.735	51	21,726	6.440	16	0.000	0.000	1
Palaemonetes transversus		0.006	15	0.000	0.000	15	0.000		7
Palaemonetes vulgaris	4.181		65	3.229	0.837	73	0.105		34
(marsh grass shrimp)		_,,		¥ 1— 3	0.00.	,,,	3.105	0.000	٠,
Panopeus herbstii	0.234	0.107	38	0.205	0.093	54	0.009	0.006	25
(Atlantic mud crab)		31247		0.202	0.020		0.007	0.000	LU
Panopeus turgidus	0.304	0.117	65	0.026	0.015	54	0.000	0.000	30
(ridgeback mud crab)	V.20.	01117	00	0.020	0.015	51	0.000	0.000	50
Petrolisthes armatus	0.015	0.012	24	0.071	0.019	29	0.000	0.000	3
(green porcelain crab)	0,0,0	0.012	2.	0.071	0.012	27	0.000	0.000	J
Petrolisthes galathinus			0	0.027	0.023	33	0.003	0.003	20
(banded porcelain crab)			v	0.027	0.025	55	0.005	0.005	20
Pinnixa chaetopterana	0.004	0.003	42	0.002	0.001	35	0.000	0.000	10
(tube pea crab)	0.001	0.005	1.2	0.002	0.001	55	0.000	0.000	10
Pinnixa cristata			0	0.000	0.000	18			0
Pinnixa lunzi	0.010	0.007	17	0.000	0.000	0			0
(Lunz pea crab)	0.010	0.007	1,			V			U
Pinnixa retinens	0.003	0.003	35	0.000	0.000	15	0.000	0.000	7
Pinnixa spp.		0.003	8	0.000	0.000	1	0.000	0.000	1
Pinnotheres maculatus	0.000	0.000	0	0.002	0.002	7	0.000	0.000	1
(squatter pea crab)			U	0.002	0.002	,			0
Rhithropanopeus harrisii	0.460	0.145	44	0.723	0.193	60	0.220	0.094	26
(Harris mud crab)	0.400	0.145	77	0.725	0.173	UU	0.220	0.094	36
Sesarma cinereum	0.000	0.000	22	0.314	0.198	61	0.043	0.036	24
(squareback marsh crab)	0.000	0.000	<i></i>	0.514	0.170	O1	0.002	0.030	34
Sesarma reticulatum	0.000	0.000	27	0.301	0.174	88	1 210	U 030	27
(heavy marsh crab)	0.000	0.000	<i>41</i>	0.501	0.174	00	1.510	0.838	37
Sesarma spp.			0	0.100	0.007	£	0.050	2.050	-
Fozeuma carolinense	1 4/1	0.474	0 70	0.120	0.097	5 5 0	2.850		2
	1.641	0.474	70	0.398	0.389	58	0.003	0.003	30
(arrow shrimp)			0	A 001	0.001	10			^
rachypenaeus constrictus (roughneck shrimp)			0	0.001	0.001	10			0
(roughneck shrimp)	^ ^ ^ ^	0.000	2.0	. . – -				5 • • •	. . -
Uca spp.	0.000	0.000	26	0.476	0.209	150	0.351	0.163	99

Table 4.—(continued).

Taxon	Inn	er mars	h	Оу	ster reef			SNB			Total	
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Pagurus annulipes			0			0			0	0.008	0.007	25
Pagurus criniticornis			0			0			0	0.296	0.104	37
Pagurus impressus			0			0	0.028	0.028	6	0.008	0.008	20
(dimpled hermit)												
Pagurus longicarpus			0			0	0.038	0.030	11	0.047	0.020	48
(longwrist hermit)												
Pagurus pollicaris			0	0.019	0.019	2	0.003	0.002	10	0.011	0.008	46
(flatclaw hermit)												
Palaemonetes intermedius	0.250	0.050	2	0.000	0.000	2	0.034	0.013	83	3.415	0.713	260
(brackish grass shrimp)												
Palaemonetes paludosus			0			0	0.000	0.000	21	0.918	0.551	58
(riverine grass shrimp)												
Palaemonetes pugio	10.441	4.002	10	0.500	0.192	2	0.933	0.213	109	23.621	2.255	324
(daggerblade grass shrimp)												
Palaemonetes spp.	0.685	0.199	5			0	0.129	0.062	18	5.028	1.432	91
Palaemonetes transversus			0			0	0.000	0.000		0.002	0.002	
Palaemonetes vulgaris	0.033	0.033	3	0.154	0.154	2	0.016	0.007	84	1.965	0.779	
(marsh grass shrimp)	27022	3,022		0.22	3,12	_	3.010	0.00.		217-02	51175	
Panopeus herbstii	0.050	0.050	2	24.596	13.904	2	0.028	0.010	6 1	0.391	0.221	182
(Atlantic mud crab)	0.000	0.000	_	2	101701	~	0.020	0.010	0.1	0.071	0.22	
Panopeus turgidus			0			0	0.001	0.000	68	0.098	0.036	217
(ridgeback mud crab)			Ť			v	0.001	0.000	00	0.070	0.000	221
Petrolisthes armatus			0	24.731	8.923	2	0.006	0.003	30	0.592	0.420	88
(green porcelain crab)			V	24.751	0.723	-	0.000	0.005	50	0.572	0.420	00
Petrolisthes galathinus			0			0	0.000	0.000	35	0.011	0.009	88
(banded porcelain crab)			V			v	0.000	0.000	55	0.011	0.003	00
Pinnixa chaetopterana			0			0	0.001	0.001	44	0.002	0.001	131
(tube pea crab)			U			v	0.001	0.001	77	0.002	0.001	131
Pinnixa cristata			0	0.000	0.000	2	0.005	0.004	17	0.002	0.002	37
Pinnixa lunzi			0	0.000	0.000	0	0.003	0.00+	0	0.002	0.002	17
•			U			V			U	0.010	0.007	17
(Lunz pea crab) Pinnixa retinens			Λ			0	0.002	0.000	21	0.002	0.001	70
	0.000	0.000	0					0.002				78
Pinnixa spp.	0.000	0.000	ι Δ			0	0.025	0.025	2	0.004	0.004	13
Pinnotheres maculatus			0			0	0.000	0.000	,	0.001	0.001	14
(squatter pea crab)	0.000	0.000	4			^	0.155	0.020	7.4	0.201	0.065	010
Rhithropanopeus harrisii	0.000	0.000	4			0	0.155	0.030	74	0.381	0.065	218
(Harris mud crab)	0.047	0.022	2			0	0.007	0.007	7.1	0.115	0.044	101
Sesarma cinereum	0.067	0.033	3			0	0.007	0.007	71	0.115	0.064	191
(squareback marsh crab)			_									
Sesarma reticulatum	1.560	0.935	5			0	0.001	0.001	97	0.326	0.139	254
(heavy marsh crab)								_			_	
Sesarma spp.	1.450	1.450	2			0	0.000	0.000		0.575	0.387	
Tozeuma carolinense			0			0	0.018	0.016	77	0.594	0.176	235
(arrow shrimp)												
Trachypenaeus constrictus			0			0	0.000	0.000	10	0.001	0.001	20
(roughneck shrimp)												
Uca spp.	9.157	4.060	7	0.000	0.000	2	0.002	0.001	169	0.377	0.111	453

Table 5.—Mean densities of fishes in different habitat types including submerged aquatic vegetation (SAV), Spartina alterniflora marsh edge (SAME), mixed vegetation marsh edge (MVME), inner marsh, oyster reef, and shallow nonvegetated bottom (SNB). Each mean density (animals per m²) was calculated as the mean of means in

Taxon		SAV			SAME			MVME	
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Fishes	13.996	1.744	75	7.712	0.812	109	14.889	3.870	40
Achirus lineatus	0.009	0.004	48	0.018	0.004	73	0.000	0.000	31
(lined sole)									
Adinia xenica	0.008	0.005	25	0.116	0.041	84	0.134	0.057	38
(diamond killifish)									
Anchoa hepsetus	0.159	0.080	43	0.000	0.000	4	0.000	0.000	1
(striped anchovy)									
Anchoa mitchilli	0.903	0.471	70	0.257	0.128	86	1.813	0.676	37
(bay anchovy)									
Anguilla rostrata			0	0.000	0.000	10	0.001	0.001	20
(American eel)									
Archosargus probatocephalus	0.027	0.014	54	0.016	0.005	74	0.005	0.004	34
(sheepshead)									
Arius felis	0.010	0.006	25	0.006	0.003	49	0.003	0.002	35
(hardhead catfish)									
Astroscopus y-graecum	0.000	0.000	8	0.000	0.000	10	0.010	0.010	20
(southern stargazer)									
Bairdiella chrysoura	0.089	0.020	66	0.125	0.049	66	0.331	0.187	36
(silver perch)									
Bathygobius soporator			0	0.006	0.006	10	0.031	0.031	20
(frillfin goby)									
Brevoortia patronus	1.447	1.262	68	0.835	0.606	76	4.967	3.833	34
(gulf menhaden)									
Chaetodipterus faber	0.000	0.000	7	0.014	0.008	36	0.000	0.000	23
(Atlantic spadefish)									
Chasmodes bosquianus	0.006	0.006	12	0.003	0.003	15	0.000	0.000	20
(striped blenny)									
Citharichthys spilopterus	0.015	0.005	56	0.007	0.003	73	0.007	0.004	36
(bay whiff)									
Cynoscion arenarius	0.037	0.037	6	0.005	0.003	22	0.000	0.000	21
(sand seatrout)									
Cynoscion nebulosus	0.107	0.022	52	0.204	0.028	89	0.039	0.018	38
(spotted seatrout)									
Cynoscion nothus			0	0.000	0.000	10	0.000	0.000	20
(silver seatrout)									
Cyprinodon variegatus	0.186	0.117	44	0.202	0.077	91	1.139	0.282	40
(sheepshead minnow)									
Dasyatis sabina	0.000	0.000	7	0.000	0.000	10	0.000	0.000	5
(Atlantic stingray)		··	. –		.	_		_	
Dormitator maculatus	0.013	0.013	15	0.000	0.000	21	0.012	0.010	10
(fat sleeper)			_			_			
Dorosoma cepedianum			0	0.000	0.000	1	0.000	0.000	2
(gizzard shad)		n n n n n				_			
Elops saurus	0.000	0.000	22	0.002	0.002	61	0.004	0.003	31
(ladyfish)									

TABLE 5.(cont.)—the database; also shown is the standard error (SE, calculated using means as observations) and the number of means (Ct = count) used in the calculation. Data are included from all seasons, salinity regimes, estuaries, and years.

Taxon	Inn	er marsh	1	Оу	ster reef			SNB			Total	
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Fishes	3.538	0.933	14	19.019	14.750	2	10.048	2.803	110	10.511	1.094	350
Achirus lineatus	0.000	0.000	1	0.000	0.000	2	0.010	0.003	9 1	0.011	0.002	246
(lined sole)												
Adinia xenica	0.776	0.328	13			0	0.000	0.000	86	0.102	0.026	246
(diamond killifish)												
Anchoa hepsetus	0.000	0.000	1			0	0.019	0.014	11	0.117	0.058	60
(striped anchovy)												
Anchoa mitchilli	0.000	0.000	9	8.423	8.423	2	2.371	0.529	108	1.368	0.239	312
(bay anchovy)												
Anguilla rostrata			0			0	0.000	0.000	14	0.001	0.001	4 4
(American eel)						_						
Archosargus probatocephalus	0.000	0.000	6	0.019	0.019	2	0.005	0.003	88	0.013	0.004	258
(sheepshead)	2.222		_								0.005	.=0
Arius felis	0.000	0.000	7			0	0.013	0.004	62	0.008	0.002	178
(hardhead catfish)										0.004	0.004	
Astroscopus y-graecum			0			0	0.000	0.000	14	0.004	0.004	52
(southern stargazer)	0.001	0.001	-	0.000	0.000	_	0.007	0.025	0.0	0.112	0.071	250
Bairdiella chrysoura	0.001	0.001	7	0.000	0.000	2	0.037	0.025	82	0.113	0.031	259
(silver perch)			0				0.000	0.000		0.016	0.014	4.4
Bathygobius soporator			0			0	0.000	0.000	14	0.016	0.014	44
(frillfin goby)	0.100	0.100	2	0.050	0.060	•	5 (00	2.600	00	2 1 45	1 111	201
Brevoortia patronus	0.100	0.100	3	0.058	0.058	2	5.608	2.698	98	3.145	1.111	281
(gulf menhaden)			0			0	0.001	0.001	43	0.005	0.003	100
Chaetodipterus faber			0			0	0.001	0.001	43	0.005	0.003	109
(Atlantic spadefish) Chasmodes bosquianus			0	0.192	0.154	2	0.000	0.000	19	0.007	0.005	68
(striped blenny)			V	0.172	0.154	۷	0.000	0.000	19	0.007	0.003	00
Citharichthys spilopterus	0.000	0.000	7			0	0.022	0.004	91	0.014	0.002	263
(bay whiff)	0.000	0.000	,			U	0.022	0.004	71	0.014	0.002	203
Cynoscion arenarius	0.000	0.000	1			0	0.014	0.007	33	0.010	0.004	83
(sand seatrout)	0.000	0.000	1			U	0.014	0.007	55	0.010	0.004	0,5
Cynoscion nebulosus	0.010	0.008	12	0.000	0.000	2	0.034	0.005	101	0.098	0.011	294
(spotted seatrout)	0.010	0.000	12	0.000	0.000	~	0.05 (0.005	101	0.020	0.011	٠, ري
Cynoscion nothus			0			0	0.001	0.001	14	0.000	0.000	44
(silver seatrout)			Ū			•	373 37	5.532				
Cyprinodon variegatus	0.728	0.312	14			0	0.060	0.044	93	0.312	0.058	282
(sheepshead minnow)									-			
Dasyatis sabina	0.000	0.000	1			0	0.006	0.004	14	0.002	0.002	37
(Atlantic stingray)												
Dormitator maculatus	0.000	0.000	5			0	0.000	0.000	24	0.004	0.003	75
(fat sleeper)		_										
Dorosoma cepedianum	0.000	0.000	1			0	0.025	0.025	2	0.008	0.008	6
(gizzard shad)												
Elops saurus	0.100	0.000	1			0	0.076	0.070	73	0.031	0.027	188
(ladyfish)												

Table 5.—(continued).

Taxon		SAV			SAME			MVME	
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
· · · · · · · · · · · · · · · · · · ·									
Etropus crossotus	0.025	0.018	6			0			0
(fringed flounder)									
Eucinostomus argenteus	0.057	0.035	65	0.006	0.002	61	0.000	0.000	33
(spotfin mojarra)									
Eucinostomus gula	0.074	0.074	6	0.005	0.004	21			0
(silver jenny)									
Eucinostomus lefroyi	0.032	0.026	15	0.001	0.001	31	0.000	0.000	7
(mottled mojarra)									
Eucinostomus melanopterus	0.257	0.000	Į	0.023	0.016	11			0
(flagfin mojarra)			_						
Eucinostomus spp.	0.148	0.148	6	0.000	0.000	2	0.000	0.000	3
Evorthodus lyricus	0.000	0.000	23	0.012	0.005	37	0.018	0.013	10
(lyre goby)	0.405	0.625			0.054				
Fundulus grandis	0.685	0.635	31	0.396	0.096	99	0.979	0.255	40
(gulf killifish)	0.000	0.000	-	0.004			0.05.		_
Fundulus jenkinsi	0.000	0.000	7	0.024	0.011	13	0.034	0.020	6
(saltmarsh topminnow)	0.050	0.000	20	0.000	0.000	= 0			
Fundulus pulvereus	0.052	0.029	22	0.028	0.008	58	0.202	0.086	35
(bayou killifish)	0.000	0.000	22	0.027	0.015	00	0.004	0.014	2.4
Fundulus similis	0.000	0.000	22	0.027	0.015	80	0.024	0.014	34
(longnose killifish)	0.025	0.025	22	0.010	0.017	20	0.061	0.055	4.6
Gambusia affinis	0.035	0.035	22	0.019	0.017	29	0.861	0.855	10
(western mosquitofish) Gobiesox strumosus	0.005	0.002	15	0.107	0.045	50	0.075	0.040	22
(skilletfish)	0.005	0.003	45	0.107	0.045	50	0.075	0.040	33
Gobioides broussoneti			0	0.011	0.000	10			0
(violet goby)			0	0.011	0.009	12			0
Gobionellus boleosoma	1.871	0.469	68	0.914	0.311	87	0.101	0.067	39
(darter goby)	1.071	0.409	00	0.314	0.511	07	0.101	0.007	39
Gobionellus oceanicus	0.003	0.003	15	0.001	0.001	31	0.000	0.000	7
(highfin goby)	0.005	0.005	15	0.001	0.001	31	0.000	0.000	,
Gobionellus shufeldti			0	0.051	0.036	24	0.004	0.004	23
(freshwater goby)			v	0.051	0.050	-,	0.001	0.001	2 2.5
Gobiosoma bosc	2.015	0.614	70	2.707	0.529	94	3.993	0.868	39
(naked goby)	•				0.0.27		2.524	V. V O O	
Gobiosoma robustum	1.876	0.438	68	0.063	0.049	51	0.014	0.010	30
(code goby)									
Harengula jaguana	0.012	0.009	12			0			0
(scaled sardine)									
Hippocampus zosterae	0.078	0.020	40			0			0
(dwarf seahorse)									
Hyporhamphus unifasciatus	0.004	0.004	19	0.003	0.003	16	0.000	0.000	23
(silverstripe halfbeak)									
Hypsoblennius ionthas			0	0.000	0.000	1			0
(freckled blenny)									
Ictalurus furcatus			0	0.000	0.000	10	0.003	0.003	20
(blue catfish)									
Ictalurus punctatus	0.000	0.000	22	0.005	0.005	21	0.000	0.000	10
(channel catfish)									
Lagodon rhomboides	2.581	0.724	70	1.275	0.235	95	0.149	0.048	36
(pinfish)									

Table 5.—(continued).

Taxon	In	ner mars	sh	Оу	ster reef			SNB			Total	
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Etropus crossotus			0			0	0.019	0.019	6	0.022	0.012	12
(fringed flounder)												
Eucinostomus argenteus	0.000	0.000	5	0.000	0.000	2	0.020	0.009	77	0.023	0.010	243
(spotfin mojarra)												
Eucinostomus gula			0			0	0.002	0.002	27	0.011	0.008	54
(silver jenny)						_						
Eucinostomus lefroyi			0			0	0.006	0.005	37	0.008	0.005	90
(mottled mojarra)			0				0.004	0.004		2.252		
Eucinostomus melanopterus			0			0	0.001	0.001	11	0.023	0.013	23
(flagfin mojarra)	0.000	0.000	2			0	0.001	0.010	10	0.040	0.020	0.2
Eucinostomus spp.	0.000	0.000	2			0	0.021	0.012	10	0.048	0.039	23
Evorthodus lyricus	0.026	0.011	5			0	0.000	0.000	39	0.007	0.002	114
(lyre goby) Fundulus grandis	0.975	0.291	14	0.000	0.000	2	0.019	0.011	97	0.407	0.088	202
(gulf killifish)	0.573	0.2.71	14	0.000	0.000	4	0.019	0.011	97	0.407	0.000	283
Fundulus jenkinsi	0.004	0.002	9			0	0.000	0.000	9	0.012	0.005	44
(saltmarsh topminnow)	0.004	0.002				V	0.000	0.000		0.012	0.003	77
Fundulus pulvereus	0.136	0.054	11	0.000	0.000	2	0.001	0.001	65	0.059	0.017	193
(bayou killifish)				0.000	0.000	_	0.001	0.031	U.D	0.057	0.017	170
Fundulus similis	0.059	0.030	6			0	0.001	0.000	82	0.015	0.006	224
(longnose killifish)										P +		
Gambusia affinis			0			0	0.000	0.000	37	0.101	0.088	98
(western mosquitofish)												
Gobiesox strumosus	0.000	0.000	2	3.442	2.750	2	0.034	0.024	66	0.087	0.035	198
(skilletfish)												
Gobioides broussoneti			0			0	0.000	0.000	12	0.006	0.005	24
(violet goby)												
Gobionellus boleosoma	0.062	0.054	13	0.000	0.000	2	0.168	0.041	96	0.748	0.143	305
(darter goby)												
Gobionellus oceanicus			0			0	0.000	0.000	36	0.001	0.001	89
(highfin goby)												
Gobionellus shufeldti	0.008	0.005	5			0	0.025	0.024	24	0.026	0.014	76
(freshwater goby)												
Gobiosoma bosc	0.012	0.007	13	4.962	1.769	2	0.956	0.232	105	2.049	0.247	323
(naked goby)							0.054					
Gobiosoma robustum			0			0	0.034	0.015	73	0.602	0.146	222
(code goby)			0				0.000	0.000	10	0.011	0.007	.
Harengula jaguana			0			0	0.009	0.009	12	0.011	0.006	24
(scaled sardine)			Ω			0			0	0.070	0.000	40
Hippocampus zosterae (dwarf seahorse)			0			0			0	0.078	0.020	40
Hyporhamphus unifasciatus			0			0	0.001	0.001	23	0.002	0.001	Q 1
(silverstripe halfbeak)			U			U	0.001	0.001	23	0.002	0.001	81
Hypsoblennius ionthas			0	0.077	0.077	2	0.000	0.000	1	0.051	0.051	4
(freckled blenny)			U	0.077	0.077	L	0.000	0.000	1	0.051	0.051	7
Ictalurus furcatus			0			0	0.000	0.000	14	0.001	0.001	44
(blue catfish)			O			v	0.000	0.000	14	0.001	0.001	77
ctalurus punctatus			0			0	0.002	0.002	30	0.002	0.001	83
(channel catfish)			ŭ			~	0.002	3,002	20	V.VV2	5.001	
Lagodon rhomboides	0.000	0.000	11	0.308	0.308	2	0.134	0.031	100	1.023	0.184	314
(pinfish)		•	- -		~ V			2.001			~~ •	·

Table 5.—(continued).

Taxon		SAV			SAME	MVME			
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Leiostomus xanthurus	0.178	0.071	68	0.062	0.023	82	0.034	0.016	37
(spot)									
Lepisosteus oculatus			0	0.000	0.000	10	0.000	0.000	20
(spotted gar)									
Lepomis cyanellus			0	0.003	0.003	9			0
(green sunfish)									
Lucania parva	0.663	0.160	60	0.543	0.246	58	1.051	0.621	17
(rainwater killifish)									
Lutjanus griseus	0.003	0.003	14	0.003	0.002	8	0.000	0.000	3
(gray snapper)									
Membras martinica	0.000	0.000	7	0.001	0.001	25	0.007	0.007	24
(rough silverside)									
Menidia beryllina	0.243	0.143	52	0.600	0.270	91	0.800	0.707	37
(inland silverside)									
Menticirrhus americanus			0	0.000	0.000	5			0
(southern kingfish)									
Menticirrhus littoralis			0	0.000	0.000	1	0.000	0.000	1
(gulf kingfish)									
Microgobius gulosus	0.077	0.047	35	0.003	0.002	58	0.007	0.007	27
(clown goby)									
Microgobius thalassinus	0.033	0.021	59	0.005	0.002	52	0.000	0.000	12
(green goby)									
Micropogonias undulatus	0.049	0.021	59	0.024	0.011	77	0.021	0.012	35
(Atlantic croaker)									
Monacanthus hispidus			0	0.010	0.010	10	0.000	0.000	20
(planehead filefish)									
Mugil cephalus	0.011	0.006	40	0.170	0.048	93	0.199	0.049	40
(striped mullet)									
Mugil curema	0.003	0.003	14	0.090	0.050	6	0.200	0.000	1
(white mullet)									
Myrophis punctatus	0.155	0.057	68	0.055	0.016	78	0.048	0.021	37
(speckled worm eel)	_	_			_				
Oligoplites saurus	0.000	0.000	13	0.013	0.010	15	0.000	0.000	3
(leatherjack)	.		_	<u> </u>		_			
Ophichthus gomesi	0.062	0.021	3	0.004	0.004	8			0
(shrimp eel)		0.015	^			-			-
Ophidion welshi	0.013	0.013	8			0			0
(crested cusk-eel)		A A==	~~	5 5	A A = -:	_ ~	-		- -
Opsanus beta	0.083	0.021	68	0.017	0.005	70	0.008	0.006	30
(gulf toadfish)	0.055	0.010	. r.≖	A A 4 4	0.00=	<i>~</i> •			
Orthopristis chrysoptera	0.052	0.018	65	0.020	0.007	61	0.001	0.001	30
(pigfish)		A A= :							
Paralichthys albigutta	0.004	0.004	8			0	•		0
(gulf flounder)					* * * -		<u> </u>	A	-
Paralichthys lethostigma	0.013	0.007	45	0.033	0.007	85	0.023	0.010	33
(southern flounder)									

TABLE 5.—(continued).

Taxon	Inne	er marsl	h	Oys	ter reef			SNB		Total		
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Leiostomus xanthurus (spot)	0.000	0.000	5	0.000	0.000	2	0.239	0.044	105	0.146	0.024	299
Lepisosteus oculatus (spotted gar)			0			0	0.002	0.002	14	0.001	0.001	44
Lepomis cyanellus (green sunfish)			0	0.173	0.173	2	0.000	0.000	9	0.020	0.018	20
Lucania parva (rainwater killifish)	0.018	0.009	1 1			0	0.013	0.009	57	0.444	0.101	203
Lutjanus griseus (gray snapper)	0.000	0.000	5			0	0.000	0.000	11	0.002	100.0	41
Membras martinica (rough silverside)	0.100	0.000	1			0	0.004	0.003	32	0.005	0.003	89
Menidia beryllina (inland silverside)	0.079	0.048	12	0.788	0.788	2	0.236	0.062	103	0.418	0.125	297
Menticirrhus americanus (southern kingfish)			0			0	0.061	0.036	5	0.030	0.020	10
Menticirrhus littoralis	0.000	0.000	1			0	0.025	0.025	2	0.010	0.010	5
(gulf kingfish) Microgobius gulosus			0			0	0.027	0.013	70	0.026	0.010	190
(clown goby) Microgobius thalassinus	0.000	0.000	1			0	0.058	0.027	62	0.031	0.011	186
(green goby) Micropogonias undulatus	0.000	0.000	7			0	0.092	0.022	91	0.052	0.010	269
(Atlantic croaker) Monacanthus hispidus			0			0	0.000	0.000	14	0.002	0.002	44
(planehead filefish) Mugil cephalus (atrined musilles)	0.465	0.179	14	0.077	0.077	2	0.036	0.007	105	0.118	0.020	294
(striped mullet) Mugil curema	0.100	0.000	1			0	0.018	0.018	11	0.033	0.013	33
(white mullet) Myrophis punctatus	0.001	0.001	8	0.019	0.019	2	0.058	0.012	99	0.077	0.015	292
(speckled worm eel) Oligoplites saurus			0			0	0.010	0.008	24	0.008	0.004	55
(leatherjack) Ophichthus gomesi			0			0	0.000	0.000	8	0.011	0.006	19
(shrimp eel) Ophidion welshi			0			0			0	0.013	0.013	8
(crested cusk-eel) Opsanus beta			0	0.096	0.096	2	0.012	0.008	85	0.033	0.007	255
(gulf toadfish) Orthopristis chrysoptera (pigfish)			0			0	0.006	0.003	75	0.022	0.006	231
(pigfish) Paralichthys albigutta (gulf flounder)			0			0			0	0.004	0.004	8
Paralichthys lethostigma (southern flounder)	0.000	0.000	6	0.000	0.000	2	0.023	0.004	92	0.024	0.003	263

Table 5.—(continued).

Taxon		SAV		<u>.</u> .	SAME			MVME	
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Poecilia latipinna (sailfin molly)	0.000	0.000	15	0.028	0.018	59	0.063	0.046	36
Pogonias cromis (black drum)	0.006	0.006	6	0.004	0.004	17	0.000	0.000	1
Pomatomus saltatrix (bluefish)			0	0.000	0.000	14			0
Pomoxis annularis (white crappie)	0.004	0.004	22	0.000	0.000	21	0.014	0.014	10
Prionotus tribulus (bighead searobin)	0.003	0.003	14	0.002	0.002	27	0.000	0.000	2
Sciaenops ocellatus (red drum)	0.096	0.054	56	0.026	0.006	82	0.010	0.006	34
Sphoeroides dorsalis (marbled puffer)			0	0.001	0.001	25	•		0
Sphoeroides parvus (least puffer)	0.000	0.000	30	0.009	0.004	50	0.006	0.004	32
Stellifer lanceolatus (star drum)	0.000	0.000	7	0.007	0.005	27	0.000	0.000	23
Strongylura marina (Atlantic needlefish)	0.009	0.009	23	0.021	0.010	25	0.009	0.007	27
Symphurus plagiusa (blackcheek tonguefish)	0.367	0.144	68	0.189	0.041	80	0.036	0.018	37
Syngnathus floridae (dusky pipefish)	0.007	0.005	27	0.013	0.012	33	0.003	0.002	27
Syngnathus louisianae (chain pipefish)	0.013	0.006	50	0.022	0.006	47	0.019	0.017	23
Syngnathus scovelli (gulf pipefish)	0.784	0.131	67	0.112	0.029	72	0.110	0.051	31
Syngnathus spp.	0.023	0.023	12			0			0
Synodus foetens (inshore lizardfish)	0.011	0.007	21	0.001	0.000	45	0.000	0.000	23
Trinectes maculatus (hogchoker)	0.000	0.000	7	0.000	0.000	13	0.000	0.000	3

Habitat of Fishery Species

Juvenile brown shrimp were most abundant during spring and summer, but they were also present in the fall. The mean size of brown shrimp was 28.4 mm TL (SE = 0.24), based on mean shrimp lengths in 2,858 Galveston Bay samples. Winter densities were very low, and the winter season was omitted in the analysis of distribution patterns. Brown shrimp habitat appeared to include all shallow estuarine areas examined (Table 7). This species was not recorded from oyster reefs, but only one mean value from summer (8 samples) was available for this biotope. Mean densities were highest in euhaline and polyhaline salinity regimes, but brown shrimp were also commonly found in fresher

Spartina alterniflora marsh edge and submerged aquatic vegetation. Mean densities of around two animals per m² were also recorded for mixed-vegetation marsh edge and shallow nonvegetated bottom. Inner marsh was not used extensively by brown shrimp.

Juvenile white shrimp were most abundant in the summer and fall. The mean TL of white shrimp was 31.8 mm (SE = 0.42), based on 1,524 Galveston Bay samples. This species was also found in most intrahabitat areas examined (Table 8). However, white shrimp were concentrated in the polyhaline and mesohaline regions of the estuaries. By far, the highest mean density occurred in SAME habitat. Relatively high densities of white shrimp

Table 5.—(continued).

Taxon	Inr	er mars	1	Oys	ster reef			SNB			Total	
(common name)	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct	Mean	SE	Ct
Poecilia latipinna (sailfin molly)	0.209	0.124	13			0	0.000	0.000	65	0.035	0.014	188
Pogonias cromis (black drum)	0.000	0.000	1			0	0.005	0.004	24	0.005	0.003	49
Pomatomus saltatrix (bluefish)			0			0	0.010	0.007	15	0.005	0.003	29
Pomoxis annularis (white crappie)			0			0	0.000	0.000	30	0.003	0.002	83
Prionotus tribulus (bighead searobin)	0.000	0.000	1	0.019	0.019	2	0.018	0.010	34	0.009	0.004	80
Sciaenops ocellatus (red drum)	0.000	0.000	10			0	0.029	0.007	92	0.038	0.012	274
Sphoeroides dorsalis (marbled puffer)			0			0	0.004	0.002	25	0.002	0.001	50
Sphoeroides parvus (least puffer)	0.000	0.000	2			0	0.025	0.008	66	0.012	0.003	180
Stellifer lanceolatus (star drum)			0			0	0.002	0.002	33	0.003	0.002	90
Strongylura marina (Atlantic needlefish)			0			0	0.000	0.000	35	0.009	0.003	110
Symphurus plagiusa (blackcheek tonguefish)	0.000	0.000	5	0.000	0.000	2	0.201	0.033	103	0.211	0.037	295
Syngnathus floridae (dusky pipefish)			0			0	0.001	0.001	44	0.006	0.003	131
Syngnathus louisianae (chain pipefish)			0			0	0.005	0.002	57	0.014	0.003	177
Syngnathus scovelli (gulf pipefish)	0.000	0.000	1	0.000	0.000	2	0.016	0.005	90	0.250	0.040	263
Syngnathus spp.			0			0			0	0.023	0.023	12
Synodus foetens (inshore lizardfish)			0			0	0.009	0.004		0.025	0.002	147
Trinectes maculatus (hogchoker)			0			0	0.003	0.002	16	0.001	0.001	39

were also collected in inner marsh, SNB, and MVME. Low mean densities were recorded for SAV, and no white shrimp were found on oyster reef.

Juvenile pink shrimp (mean TL = 19.8 mm, SE = 0.48, based on 442 Galveston Bay samples) were present mainly in the summer and fall, and this species was generally less abundant than either brown shrimp or white shrimp. Pink shrimp habitat also appeared to be more restricted than the other commercially important shrimps (Table 9). Densities were low in oligohaline areas, and no pink shrimp were found in inner marsh or on oyster reefs. Mean pink shrimp densities were highest in the polyhaline salinity regime and in SAV and marsh edge.

In recording data on the gulf stone crab, I assumed that all specimens in Texas and Louisiana were *Menippe adina*, although some crabs were reported as its congener *M. mercenaria* (the eastern Gulf species). Both juvenile and adult gulf stone crabs inhabit these estuaries, but juveniles were dominant in the samples. The mean carapace width (CW) was 26.7 mm (SE = 3.49), based on 40 Galveston Bay samples; the largest specimen was 88 mm CW. This species was found almost exclusively on oyster reefs (Table 4). The limited sampling in this biotope prevented an analysis of seasonality or an examination of distribution patterns in relation to salinity; samples

Table 6.—Dominant taxa collected in different estuarine habitat types. For each habitat type, the 10 most abundant decapod crustaceans and fishes are listed in rank order based on mean densities.

Rank	Submerged aquatic vegetation	Spartina alterniflora edge marsh	Mixed vegetation edge marsh	Inner marsh	Oyster reef	Shallow non- vegetated bottom
			Decapod Crustac	eans		
1	Callinectes spp.	Palaemonetes pugio	Palaemonetes pugio	Uca spp.	Petrolisthes armatus	Callinectes spp.
2	Palaemonetes spp.	Palaemonetes spp.	Sesarma spp.	Palaemonetes pugio	Panopeus herbstii	Farfantepenaeus aztecus
3	Palaemonetes pugio	Farfantepenaeus aztecus	Callinectes sapidus	Sesarma spp.	Eurypanopeus depressus	Litopenaeus setiferus
4	Farfantepenaeus aztecus	Callinectes sapidus	Farfantepenaeus aztecus	Litopenaeus setiferus	Alpheus heterochaelis	Palaemonetes pugio
5	Palaemonetes intermedius	Callinectes spp.	Litopenaeus setiferus	Palaemonetes spp.	Menippe adina	Callinectes sapidus
6	Hippolyte zostericola	Litopenaeus setiferus	Uca spp.	Callinectes sapidus	Clibanarius vittatus	Palaemonetes spp.
7	Callinectes sapidus	Palaemonetes intermedius	Farfantepenaeus duorarum	Farfantepenaeus aztecus	Palaemonetes pugio	Acetes americanus
8	Palaemonetes vulgaris	Uca spp.	Palaemonetes intermedius	Palaemonetes intermedius	Callinectes sapidus	Rhithropanopeus harrisii
9	Dyspanopeus texana	Palaemonetes vulgaris	Dyspanopeus texana	Panopeus herbstii	Palaemonetes vulgaris	Farfantepenaeus duorarum
10	Tozeuma carolinense	Palaemonetes paludosus	Macrobrachium ohione	Clibanarius vittatus	Pagurus pollicaris	Callinectes similis
			Fishes			
1	Lagodon rhomboides	Gobiosoma bosc	Brevoortia patronus	Fundulus grandis	Anchoa mitchilli	Brevoortia patronus
2	Gobiosoma bosc	Lagodon rhomboides	Gobiosoma bosc	Adinia xenica	Gobiosoma bosc	Anchoa mitchilli
3	Gobiosoma robustum	Gobionellus boleosoma	Anchoa mitchilli	Cyprinodon variegatus	Gobiesox strumosus	Gobiosoma bosc
4	Gobionellus boleosoma	Brevoortia patronus	Cyprinodon variegatus	Mugil cephalus	Menidia beryllina	Leiostomus xanthurus
5	Brevoortia patronus	Menidia beryllina	Lucania parva	Poecilia latipinna	Pomatomus saltatrix	Menidia beryllina
6	Anchoa mitchilli	Lucania parva	Fundulus grandis	Fundulus pulvereus	Lepomis cyanellus	Symphurus plagiusa
7	Syngnathus scovelli	Fundulus grandis	Gambusia affinis	Brevoortia patronus	Lagodon rhomboides	Gobionellus boleosoma
8	Fundulus grandis	Anchoa mitchilli	Menidia beryllina	Mugil curema	Opsanus beta	Lagodon rhomboides
9	Lucania parva	Cynoscion nebulosus	Bairdiella chrysoura	Membras martinica	Chasmodes bosquianus	Micropogonias undulatus
10	Symphurus plagiusa	Cyprinodon variegatus	Fundulus pulvereus	Elops saurus	Mugil cephalus	Elops saurus

on oyster reefs were available only in summer and winter in the polyhaline salinity regime of Galveston Bay. Densities presented here may be underestimated due to inadequate sampling; Valentine et al. (1994) reported that stone crabs found near edges of sea grass beds burrowed as deep as 1.25 m into the substrate.

Blue crabs also inhabit estuaries as juveniles and adults. Although specimens as large as 128 mm CW were collected, most blue crabs were small juveniles (mean CW = 16.3 mm, SE = 0.30, based on

1,432 Galveston Bay samples). These juveniles were present in every estuarine area sampled (Table 10); they were most abundant in fall but were found throughout the year. Mean densities of blue crabs were lowest in the euhaline salinity regime (mainly SAV habitat of South Texas). The highest mean densities were found in polyhaline and mesohaline SAV and SAME. Mixed-vegetation marsh edge also appeared to support relatively high densities of this species, while inner marsh, SNB, and oyster reefs had relatively low mean densities.

TABLE 7.—Density (per m²) of brown shrimp Farfantepenaeus aztecus in different intrahabitat areas characterized by habitat type and salinity regime. The mean densities and standard errors (SE) were calculated using means in the database as the observations. The count represents the number of means in each calculation. Only data from spring, summer, and fall are included.

			Salinity	regime	· · · · ·	
Habitat type	Statistic	Euhaline	Polyhaline	Mesohaline	Oligohaline	Total
Submerged aquatic	Mean	5.68	11.03	5.71	0.08	7.20
vegetation	SE	0.96	1.94	2.93	0.08	1.02
	Count	20	21	5	6	52
Spartina alterniflora	Mean	8.56	10.44	4.02	3.43	8.31
marsh edge	SE	0.00	0.94	0.79	1.43	0.74
	Count	1	62	24	6	93
Mixed vegetation	Mean		3.94	3.42	1.45	2.60
marsh edge	SE		2.25	1.10	0.35	0.57
	Count	0	5	17	18	40
Inner marsh	Mean		2.00	0.21		0.49
	SE		1.40	0.09		0.26
	Count	0	2	11	0	13
Oyster reef	Mean		0.00			0.00
	SE		0.00			0.00
	Count	0	1	0	0	1
Shallow nonvegetated	Mean		2.50	1.34	0.83	1.99
bottom	SE		0.28	0.27	0.33	0.20
	Count	0	62	23	14	99
All habitats	Mean	5.82	6.91	2.70	1.33	4.88
	SE	0.92	0.58	0.42	0.29	0.35
	Count	21	153	80	44	298

Juvenile red drum (mean TL = 51.3 mm, SE = 7.67, based on 133 Galveston Bay samples) were abundant in the fall and also present in winter samples. This species was mainly found in polyhaline and euhaline salinity regimes (Table 11). By far, the highest mean density of red drum was found in polyhaline SAV. In contrast, no red drum were found in mesohaline or oligohaline SAV. Moderate densities were recorded in polyhaline SAME and SNB. Red drum were absent on oyster reefs and rare in inner marsh or MVME.

Gray snapper were rare in the estuarine areas examined; only four juveniles were recorded from the Galveston Bay and Terrebonne and Timbalier Bay systems. The overall mean density from Table 5 was around 16 fish per ha, but if you assumed that whenever gray snapper were not reported in a study the densities were zero (i.e., all fish specimens collected in the various studies were correctly identified and reported), this density would be around 2 fish per ha. Gray snapper were only recorded from polyhaline SAV and mesohaline SAME.

Bluefish were also rare; only five juveniles were collected from Galveston Bay, all on SNB. The overall mean density for this species in Table 5 was

around 50 fish per ha, but again, if you recorded a density of zero whenever this species was not reported in a study, the mean density would be considerably lower (around 4 fish per ha). Zimmerman et al. (1989) reported a density of 0.42 bluefish per m² on oyster reefs, but this value was in error; I reviewed the original data analyzed in the study and found no record of this species in the samples.

Juvenile spotted seatrout were found in all estuaries sampled and were commonly collected in summer and fall. The mean TL for this species was 48.7 mm (SE = 1.75), based on 265 Galveston Bay samples; the largest specimen collected in these samples was 145 mm TL. Spotted seatrout were concentrated in the high-salinity regions (Table 12). The highest mean density occurred in SAME followed by SAV. There was also a high mean density in MVME when it occurred in the polyhaline salinity regime. Juvenile spotted seatrout were not found on oyster reefs and were rare in inner marsh and in all oligohaline areas.

Most southern flounder were found in the spring and summer, but the species was present in estuarine habitats throughout the year. The mean TL of southern flounder was 127.2 mm (SE = 9.06), based

TABLE 8.—Density (per m²) of white shrimp *Litopenaeus setiferus* in different intrahabitat areas characterized by habitat type and salinity regime. The mean densities and standard errors (SE) were calculated using means in the database as the observations. The count represents the number of means in each calculation. Only data from summer and fall are included.

			Salinity	regime		
Habitat type	Statistic	Euhaline	Polyhaline	Mesohaline	Oligohaline	Total
Submerged aquatic	Mean	0.30	1.51	0.36	0.12	0.80
vegetation	SE	0.07	0.37	0.33	0.12	0.19
	Count	15	17	4	4	40
Spartina alterniflora	Mean		10.31	8.66	1.22	9.41
marsh edge	SE		1.77	4.02	0.61	1.60
	Count	0	39	14	3	56
Mixed vegetation	Mean		5.00	2.04	0.34	1.60
marsh edge	SE		3.82	0.94	0.16	0.61
	Count	0	3	11	12	26
Inner marsh	Mean		9.90	1.33		2.40
	SE		0.00	0.77		1.26
	Count	0	1	7	0	8
Oyster reef	Mean		0.00			0.00
	SE		0.00			0.00
	Count	0	1	0	0	1
Shallow nonvegetated	Mean		2.23	2.05	0.13	1.91
bottom	SE		0.54	0.52	0.07	0.38
	Count	0	43	15	9	67
All habitats	Mean	0.30	5.27	3.63	0.34	3.78
	SE	0.07	0.81	1.19	0.11	0.54
	Count	15	104	51	28	198

on 90 Galveston Bay samples, and the largest specimen was 395 mm TL. Southern flounder were collected in samples from 7 of the 10 estuaries in the database. The highest mean density of this species was in SAME followed by MVME, SNB, and SAV (Table 13). No southern flounder were recorded from inner marsh or oyster reef.

Sand seatrout (mean TL = 39.9 mm, SE = 3.08, based on 34 Galveston Bay samples) were found only in Galveston and Lavaca Bays, in polyhaline and mesohaline salinity regimes, and during spring, summer, and fall. The highest mean density was in SAV, and the mean density was also relatively high on SNB (Table 5).

Discussion

The essential fish habitat requirements of the Magnuson-Stevens Act represent a recognition of the importance of habitats to fishery resources, provide an opportunity to enhance protection for fish habitats, and promote awareness of the role habitat characteristics play in fishery ecology. However,

accurately delineating the habitat of a fishery species (or a particular life stage) requires a detailed and comprehensive assessment of where these animals live. In addition, the linkages between habitats and fishery production are complex, and the identification of intrahabitat areas as EFH is likely to be complicated.

In developing guidelines for identifying EFH, the National Marine Fisheries Service considered different levels of information available on interactions between habitats and fishery species (62 FR 66531) (NMFS 1997). The most basic information is presence and absence or frequency-of-occurrence data on the distribution of a fishery species. These data can be used to define the geographic range of a species; they also can be used to delineate the habitat of a species (where it lives) if sampling effort is adequate. However, a more informative examination of habitat-use patterns requires the measurement of relative densities in different intrahabitat areas. In addition, the only way to make legitimate comparisons among different biotopes and across different studies using different gear types is to measure actual densities of fishery species. In this pa-

TABLE 9.—Density (per m²) of pink shrimp Farfantepenaeus duorarum in different intrahabitat areas characterized by habitat type and salinity regime. The mean densities and standard errors (SE) were calculated using means in the database as the observations. The count represents the number of means in each calculation. Only data from summer and fall are included.

			Salinity regime		
Habitat type	Statistic	Polyhaline	Mesohaline	Oligohaline	Total
Submerged aquatic	Mean	3.55	0.22	0.10	2.12
vegetation	SE	1.76	0.22	0.10	1.08
	Count	11	4	4	19
Spartina alterniflora	Mean	1.78	2.02	0.54	1.73
marsh edge	SE	0.40	1.24	0.37	0.38
	Count	31	8	3	42
Mixed vegetation	Mean	2.37	1.06	0.16	0.74
marsh edge	SE	2.37	1.00	0.11	0.43
	Count	3	6	12	21
Inner marsh	Mean	0.00			0.00
	SE	0.00			0.00
	Count	1	0	0	1
Oyster reef	Mean	0.00			0.00
	SE	0.00			0.00
	Count	1	0	0	1
Shallow nonvegetated	Mean	0.24	0.17	0.01	0.19
bottom	SE	0.07	0.08	0.01	0.04
	Count	33	11	9	53
All habitats	Mean	1.36	0.87	0.15	1.01
	SE	0.32	0.41	0.07	0.21
	Count	80	29	28	137

per, I examined density patterns in shallow-water estuarine systems of Texas and Louisiana using available data collected with quantitative enclosure sampling devices. Enclosure samplers, which include throw traps, drop samplers, lift nets, and flume weirs, have high and relatively stable catch efficiencies and provide comparable density estimates for small nekton in different estuarine biotopes (Kneib 1997; Rozas and Minello 1997).

Historically, otter trawls commonly have been used for monitoring populations of fishery species in estuaries because of their relative ease of use, large areas swept, and clean samples. The data collected with trawls, however, are generally inappropriate for comparing densities among estuarine biotopes and conducting a detailed examination of habitat-use patterns. Trawls and other towed nets have low and variable catch efficiency. This efficiency varies in relation to the species and size of target animals (Kjelson and Johnson 1978; Lyons 1986; Hartman and Herke 1987; Parsley et al. 1989; Allen et al. 1992; Millar 1992) and the method of rigging, mesh size, noise of boat, towing speed and direction, tow duration, and method of net

retrieval (Kashkin and Parin 1983; Thayer et al. 1983; Carothers and Chittenden 1985; Creutzberg et al. 1987; DeAlteris et al. 1989; Millar 1992; Engas 1994; Workman et al. 1995).

Catch efficiency of towed nets varies with many habitat characteristics including:

- presence of vegetation (Miller et al. 1980; Howard and Lowe 1984; Gray and Bell 1986; Leber and Greening 1986; Orth and van Montfrans 1987);
- light (Glass and Wardle 1989; Engas 1994; Michalsen et al. 1996);
- turbidity (Nielsen 1983);
- temperature (Allen et al. 1992);
- water depth (Rogers 1985; Hartman and Herke 1987;
 Bishop and Khan 1991; Loneragan et al. 1995); and
- substrate type (Krieger 1993).

For species that burrow in the substrate such as penaeid shrimps and some crabs, catch efficiency of towed nets will vary with all of the environmental factors that affect burrowing. Burrowing behavior of penaeids has been shown to be affected by:

TABLE 10.—Density (per m²) of blue crab *Callinectes sapidus* in different intrahabitat areas characterized by habitat type and salinity regime. The mean densities and standard errors (SE) were calculated using means in the database as the observations. The count represents the number of means in each calculation. Data from all seasons are included.

			Salinity	regime		
Habitat type	Statistic	Euhaline	Polyhaline	Mesohaline	Oligohaline	Total
Submerged aquatic	Mean	0.76	13.04	5.58	1.60	5.05
vegetation	SE	0.17	2.89	3.67	0.92	1.16
	Count	35	21	5	6	67
Spartina alterniflora	Mean	1.63	6.08	7.20	4.79	6.24
marsh edge	SE	0.00	0.51	2.58	2.81	0.75
	Count	1	68	25	6	100
Mixed vegetation	Mean		3.23	1.94	3.27	2.70
marsh edge	SE		2.10	0.91	1.72	0.89
	Count	0	5	17	18	40
Inner marsh	Mean		1.15	0.42		0.53
	SE		0.45	0.10		0.12
	Count	0	2	12	0	14
Oyster reef	Mean		0.23			0.23
	SE		0.08			0.08
	Count	0	2	0	0	2
Shallow nonvegetated	Mean		0.96	0.90	0.61	0.90
bottom	SE		0.09	0.36	0.22	0.10
	Count	0	72	23	14	109
All habitats	Mean	0.79	4.56	3.25	2.40	3.54
	SE	0.17	0.51	0.89	0.82	0.36
	Count	36	170	82	44	332

- shrimp size (Dall 1958; Hughes 1968; Kurata 1981; Kenyon et al. 1995; Primavera and Lebata 1995; Liu and Loneragan 1997);
- light (Fuss and Ogren 1966; Wickham and Minkler 1975; Bishop and Herrnkind 1976);
- moon phase (Fuss and Ogren 1966; Bishop and Herrnkind 1976);
- food availability (Dall 1958);
- dissolved oxygen (Egusa and Yamamoto 1961);
- presence of predators (Fuss and Ogren 1966);
- pressure and water depth (Hughes 1966;
 Wickham 1967; Vance 1992);
- salinity (Lakshmi et al. 1976);
- temperature (Fuss and Ogren 1966; Aldrich et al. 1968; Hill 1985);
- sea grass type (Kenyon et al. 1995);
- substrate type (Williams 1958; Moller and Jones 1975; Aziz and Greenwood 1982);
- weather (Fuss and Ogren 1966);
- molting (Wassenberg and Hill 1984);
- endogenous rhythms (Wickham 1967; Hughes 1968, 1969; Bishop and Herrnkind 1976); and
- ammonia concentrations (Allan and Maguire 1995).

Unless one compensates for changing gear efficiency with habitat characteristics, one can never be sure whether differences in catch are due to density patterns of a target species or to gear selectivity.

The database developed for analysis in this study combines information from 22 research projects on animal densities in estuaries of Texas and Louisiana. This type of meta-analysis can provide valuable insights into patterns of species distribution, but by necessity the analysis is general in nature. To some degree, the results are dependent upon the distribution of samples in relation to intrahabitat areas. Although a large number (5,149) of enclosure samples were included in the database, patterns of animal densities and habitat use can be influenced by the distribution of samples among estuaries, salinity regimes, seasons, and habitat types. I tried to take these sampling patterns into consideration when reporting and interpreting the data.

Perhaps the most striking pattern apparent in the data was the high density of decapod crustaceans in relation to fishes. The highest overall mean density for all species was for daggerblade grass shrimp

TABLE 11.—Density (per m²) of red drum *Sciaenops ocellatus* in different intrahabitat areas characterized by habitat type and salinity regime. The mean densities and standard errors (SE) were calculated using means in the database as the observations. The count represents the number of means in each calculation. Only data from fall and winter are included.

			Salinity	regime		·	
Habitat type	Statistic	Euhaline	Polyhaline	Mesohaline	Oligohaline	Total	
Submerged aquatic	Mean	0.096	0.457	0.000	0.000	0.213	
vegetation	SE	0.062	0.281	0.000	0.000	0.118	
	Count	8	10	4	3	25	
Spartina alterniflora	Mean		0.057	0.010	0.032	0.043	
marsh edge	SE		0.018	0.007	0.032	0.013	
	Count	0	25	10	3	38	
Mixed vegetation	Mean		0.000	0.000	0.012	0.006	
marsh edge	SE		0.000	0.000	0.012	0.006	
	Count	0	2	5	8	15	
Inner marsh	Mean			< 0.001		< 0.001	
	SE			< 0.001		< 0.001	
	Count	0	0	3	0	3	
Oyster reef	Mean		0.00			0.00	
	SE		0.000			0.000	
	Count	0	1	0	0	1	
Shallow nonvegetated	Mean		0.067	0.030	0.000	0.049	
bottom	SE		0.020	0.024	0.000	0.014	
	Count	0	28	8	7	43	
All habitats	Mean	0.096	0.120	0.011	0.009	0.073	
	SE	0.062	0.046	0.007	0.006	0.025	
	Count	8	66	30	21	125	

Palaemonetes pugio at 23.6 organisms per m²; the mean density for this species in Spartina alterniflora marsh edge was 58.8 organisms per m². For fishery species (not all under federal management plans), overall mean densities per m² were 4.61 for brown shrimp, 3.54 for blue crab, 3.14 for gulf menhaden, 2.37 for white shrimp, 0.67 for pink shrimp, 0.15 for spot, 0.10 for spotted seatrout, 0.04 for red drum, 0.02 for gulf stone crab, and 0.02 for southern flounder. Bluefish and gray snapper (<0.01 per m²) were reported in relatively few studies, and their actual overall densities would be considerably lower than those reported in this analysis if the fish were recorded as having zero densities (as is likely) in the other studies examined.

On the basis of mean densities in the six habitat types examined, *Spartina alterniflora* marsh edge was used most by brown shrimp, white shrimp, blue crab, spotted seatrout, and southern flounder. Pink shrimp, red drum, and sand seatrout were most abundant in submerged aquatic vegetation. Stone crab had highest mean densities on oyster reef and gulf menhaden on shallow nonvegetated bottom. Each of the six habitat types examined in my analysis

ranked first or second in use by at least one fishery species (Tables 4 and 5). The data indicate, therefore, that all estuarine areas examined are likely to be essential for some fishery species.

Few other studies in Gulf of Mexico estuaries provide nekton density comparisons for two or more of the habitat types examined in my analysis. Baltz et al. (1993) showed that marsh edge was used extensively by estuarine fishes in the Barataria Bay system of Louisiana; the 15 most abundant species sampled in their study (including red drum, gulf menhaden, spot, and spotted seatrout) were concentrated at the marsh-water ecotone. In Alabama, Williams et al. (1990) reported that blue crab densities were significantly higher in sea grass than on nonvegetated bottom. Sheridan (1992) compared nekton densities among sea grass, nonvegetated bottom, and mangrove prop roots in Rookery Bay, Florida. Sheridan et al. (in press) compared sea grass and nonvegetated bottom in Florida Bay; densities of pink shrimp and blue crab were highest in sea grass. In Florida, Valentine et al. (1994) reported stone crab densities to be highest at the edge of sea grass beds (0.8–6.0 crabs per m²).

Table 12.—Density (per m²) of spotted seatrout *Cynoscion nebulosus* in different intrahabitat areas characterized by habitat type and salinity regime. The mean densities and standard errors (SE) were calculated using means in the database as the observations. The count represents the number of means in each calculation. Only data from summer and fall are included.

			Salinity	regime		
Habitat type	Statistic	Euhaline	Polyhaline	Mesohaline	Oligohaline	Total
Submerged aquatic	Mean	0.113	0.240	0.144	0.000	0.160
vegetation	SE	0.180	0.050	0.083	0.000	0.033
	Count	9	14	4	4	31
Spartina alterniflora	Mean		0.415	0.181	0.000	0.333
marsh edge	SE		0.045	0.059	0.000	0.038
	Count	0	36	13	3	52
Mixed vegetation	Mean		0.288	0.040	0.000	0.051
marsh edge	SE		0.167	0.020	0.000	0.026
	Count	0	3	10	12	25
Inner marsh	Mean		0.100	0.003		0.017
	SE		0.000	0.003		0.014
	Count	0	1	6	0	7
Oyster Reef	Mean		0.00			0.00
	SE		0.000			0.000
	Count	0	1	0	0	1
Shallow nonvegetated	Mean		0.059	0.023	0.024	0.046
bottom	SE		0.009	0.015	0.014	0.007
	Count	0	40	13	9	62
All habitats	Mean	0.113	0.227	0.079	0.008	0.149
	SE	0.180	0.025	0.021	0.005	0.016
	Count	9	95	46	28	178

Density patterns provide information on the intrahabitat areas used most extensively by a fishery species, but determining whether a habitat is essential for a species is more difficult. If intrahabitat areas are ranked on the basis of nekton density, there is no strong basis for deciding where to draw the line between essential and nonessential areas. However, intrahabitat areas with the highest densities are most likely to be essential for that species. An argument can be made that the entire habitat of a species is essential. This contention is supported if intrahabitat areas are essential not only for sustaining production of a fishery on the species but also for supporting the ecological contribution of the species to marine ecosystems. However, identifying every place where a species lives as EFH is not likely to enhance our ability to protect specific intrahabitat areas that are most essential in maintaining fishery productivity. Therefore, to help provide additional focus to conservation efforts, the interim final rule to implement the EFH policy also recognizes that some EFH may be identified as habitat areas of particular concern (HAPC) (NMFS 1997). These HAPC

would be particularly important to the long-term productivity of a fishery species, or they would be particularly vulnerable to degradation.

In shallow estuarine areas of Texas and Louisiana, brown shrimp were concentrated in SAV and SAME (Table 7), and these intrahabitat areas are likely to be an HAPC for this species. White shrimp densities were high in most marsh habitats and nearby SNB (Table 8); thus, the entire marsh biotope appeared to be an HAPC for this species. For red drum, SAV in high-salinity areas of the bays might be HAPC, but the data available for determining habitat-use patterns for this species are still inconclusive (Table 11). For other managed fishery species that use estuarine nurseries in the Gulf of Mexico such as pink shrimp, bluefish, stone crab, and gray snapper, the data available for my analysis of habitat-use patterns are probably insufficient to make decisions on HAPC. In part, the inadequacy of available data are due to low densities caused by the geographic range of these species being centered in other areas. Data analyses from other Gulf estuaries may improve the database in this regard. For example,

TABLE 13.—Density (per m²) of southern flounder *Paralichthys lethostigma* in different intrahabitat areas characterized by habitat type and salinity regime. The mean densities and standard errors (SE) were calculated using means in the database as the observations. The count represents the number of means in each calculation. Data from all seasons are included.

	•		Salinity	regime		·-
Habitat type	Statistic	Euhaline	Polyhaline	Mesohaline	Oligohaline	Total
Submerged aquatic	Mean	0.015	0.018	0.000	0.000	0.013
vegetation	SE	0.014	0.010	0.000	0.000	0.007
	Count	18	16	5	6	45
Spartina alterniflora	Mean		0.028	0.055	0.000	0.033
marsh edge	SE		0.005	0.027	0.000	0.007
	Count	0	59	20	6	85
Mixed vegetation	Mean		0.048	0.023	0.017	0.023
marsh edge	SE		0.048	0.018	0.010	0.010
	Count	0	4	11	18	33
Inner marsh	Mean		0.000	0.000	•	0.000
	SE		0.000	0.000		0.000
	Count	0	1	5	0	6
Oyster reef	Mean		0.000			0.000
	SE		0.000			0.000
	Count	0	2	0	0	2
Shallow nonvegetated	Mean		0.027	0.023	0.005	0.023
bottom	SE		0.005	0.007	0.004	0.004
	Count	0	59	19	14	92
All habitats	Mean	0.015	0.027	0.030	0.009	0.024
	SE	0.014	0.003	0.010	0.005	0.003
	Count	18	141	60	44	263

gag Mycteroperca microlepis were not reported in any of the studies included in my analysis, but Koenig and Coleman (1998) measured densities between 0.042 and 0.055 fish per m² in sea grass beds of St. George Sound, Florida.

For many reasons, the delineation of habitat and the identification of essential intrahabitat areas should not be based solely on the density data in this analysis. All estuarine areas available to fishery species in Texas and Louisiana have not been adequately sampled. For example, few quantitative density estimates are available for deep (>1 m water depth) areas of these bays, although Hellier (1958), Jones et al. (1963), and Jones (1965) used large enclosure samplers to estimate fish biomass in Corpus Christi Bay. Tidal freshwater regions of these estuaries also have been infrequently sampled, although Castellanos (1997) documented extensive use of these habitats by blue crabs Callinectes sapidus in the Atchafalaya River Delta of Louisiana. The data included in my analysis on use of oyster reefs (Zimmerman et al. 1989) were limited in scope and probably do not adequately reflect the value of this biotope to managed fishery species. On the South Atlantic coast of the United States, brown shrimp, white shrimp, pink shrimp, blue crab, red drum, gray snapper, bluefish, and gag have all have been found on oyster reefs (Wenner et al. 1996; Coen et al. 1999, this volume). In Gulf of Mexico estuaries outside Texas and Louisiana, other biotopes may be important for fishery species. For example, mangroves (Thayer et al. 1987; Sheridan 1992; Mullin 1995; Thayer and Sheridan, in press); calcium carbonate rock (Beck 1995); macroalgae beds (Herrnkind and Butler 1994); and sponge communities (Herrnkind et al. 1995) may be highly utilized in Florida estuaries.

Densities of fishery species are often centered in community habitats or biotopes, but there can be substantial variability within biotopes. In the salt marsh, for example, both the distance to the marsh—water interface and the extent of tidal inundation affect nekton density patterns (Rozas and Reed 1993; Minello et al. 1994; Peterson and Turner 1994; Minello and Webb 1997). McIvor and Rozas (1996) summarized patterns of salt-marsh use by nekton and discussed factors affecting this use. In sea grass beds, wave energy has been shown to affect use by pink

shrimp (Murphey and Fonseca 1995), and the amount of edge affects use by red drum (Holt et al. 1983). Rooker (1997) and Sheridan et al. (in press) showed that nekton had different densities in Halodule wrightii sea grass beds compared with Thalassia testudinum, but Fonseca et al. (1996) found few differences in nekton densities among three species of sea grasses in Tampa Bay. Regional differences in habitat use also exist, and salt marshes of the southeastern United States appear to support much lower nekton densities than marshes on the Gulf coast (Rozas 1993; Wenner and Beatty 1993; Kneib 1997). Heck and Coen (1995) also reported regional differences in predation intensity in sea grass habitats. These patterns need to be examined with a directed sampling program.

Tidal flooding patterns also complicate the measurement of density and the identification of EFH in estuaries. The marsh surface is intertidal and only available for a portion of each tidal cycle. Densities measured in my analysis were almost all conducted at high tide when all habitat types were available for exploitation. However, fishery species using intertidal marsh at high tide must retreat into adjacent subtidal areas at low tide. In the northern Gulf of Mexico, astronomical tides are small, and meteorological events often control tidal flooding. Many salt marshes in this re-

gion are subsiding, and the marsh surface is flooded for extensive periods throughout the year (Rozas and Reed 1993). Over a 1-year period in Galveston Bay (1990–1991), the marsh edge was flooded 78.1% of the time, and inner marsh was flooded 66.3% of the time (Minello and Webb 1997). A seasonal pattern in tidal flooding is also apparent with the highest flooding durations during the spring and fall (Figure 2).

Although density patterns provide insights into the value of intrahabitat areas for fishery species, the determination of EFH probably should not be based on these distribution data alone. Information on functional relationships between habitats and fishery species is required to more accurately assess habitat value, and data on survival, growth, and reproductive success in different intrahabitat areas should be used to assess EFH. A limited amount of these data are available for federally managed fishery species that use estuaries of the northern Gulf of Mexico. Stone crabs have an affinity for structured habitats, and Beck (1995, 1997) showed that structure and shelter increased growth, survival, and fecundity for this species. Both brown shrimp and white shrimp have high densities in vegetated areas, but only brown shrimp exhibited increased growth within salt marsh vegetation compared with shallow nonvegetated bottom; white shrimp growth was

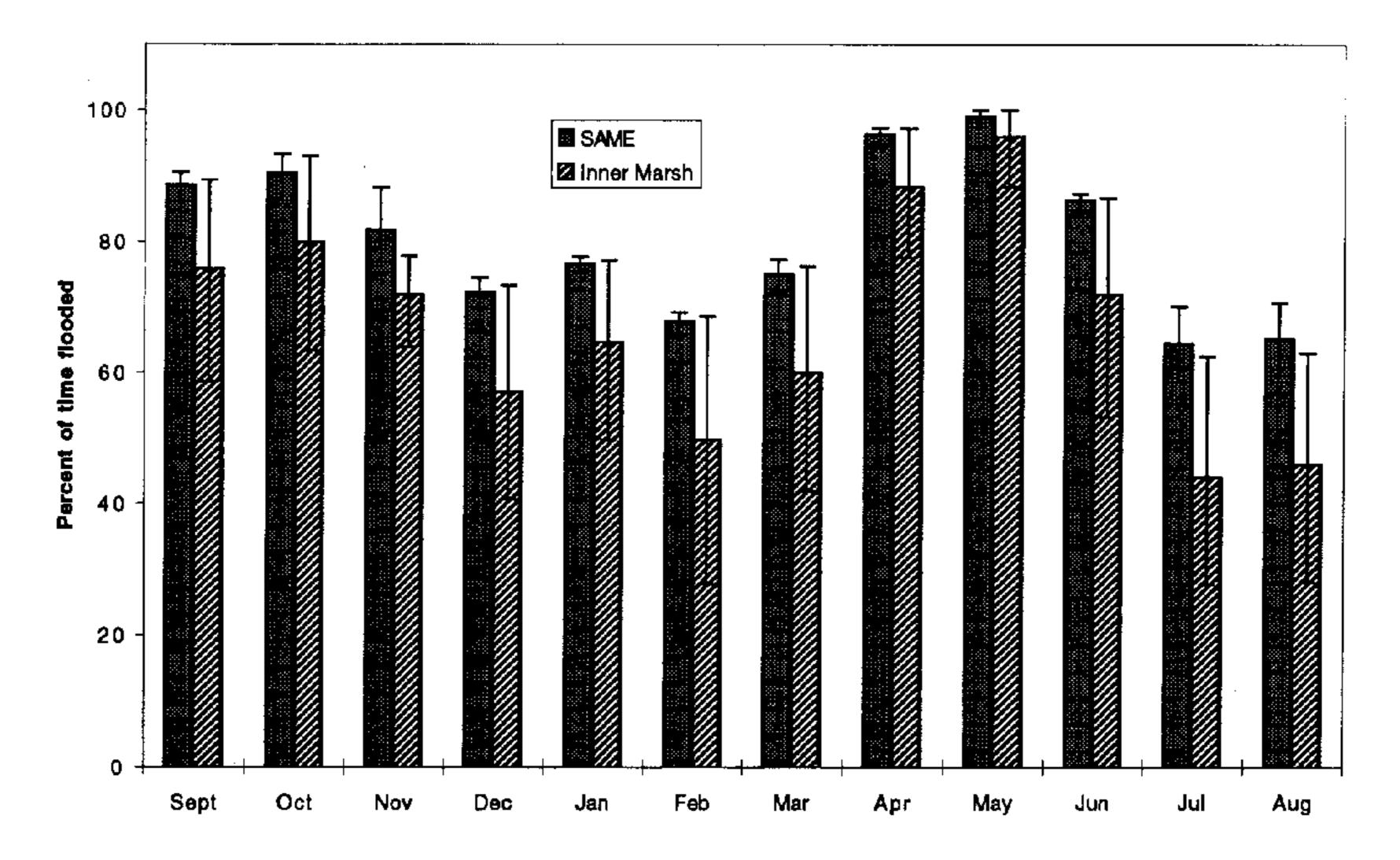


FIGURE 2.—Seasonal pattern of tidal inundation at *Spartina alterniflora* marsh edge (SAME) and inner marsh habitat types in lower Galveston Bay, Texas. Bar heights represent the mean percentage of time during each month that the habitat types were flooded in 1990–1991. Vertical lines through bars show the range for the five marshes examined. Adapted from Minello and Webb (1997).

similar between these intrahabitat areas (Minello and Zimmerman 1991). Vegetative structure also appears to reduce fish predation on juvenile brown shrimp (Minello and Zimmerman 1983; Minello et al. 1989), and survival time for tethered brown shrimp was higher in SAV and SAME compared with nonvegetated sand bottom (Minello 1993). Growth of red drum appears similar between sea grass and sand bottom (Nadeau 1991; Rooker et al. 1997), while survival of juvenile red drum was higher in SAV compared with nonvegetated bottom (Rooker et al. 1998). In estuaries of southern Florida, the structure of algae, sea grasses, and sponges has been shown to increase survival of juvenile Caribbean spiny lobsters Panulirus argus (Herrnkind and Butler 1986; Childress and Herrnkind 1994; Butler et al. 1995; Herrnkind et al. 1997). Similar comparative studies are needed for other habitats and other managed fishery species. Ideally, these kinds of data will be synthesized to determine relationships between productivity and the different intrahabitat areas used by fishery species.

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